

EVIDENCE FOR THE LOW-ALTITUDE ORIGIN OF THE  
CAPE MOUNTAIN BIOME DERIVED FROM THE SYSTEMATIC  
REVISION OF THE GENUS *COLOPHON* GRAY  
(COLEOPTERA, LUCANIDAE)

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(With 31 figures)

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ABSTRACT

The Cape high-mountain stag beetles have been studied during the past five years. They are recognized as representatives of a biome restricted today to the high-altitude ranges of the mountains. This biome is often referred to as a mountain relict. An evaluation of the kinship relations of the *Colophon* species presented a distribution pattern where closely related species are isolated on mountain ranges separated by wide stretches of low-altitude plainland. These plains are now uninhabitable for *Colophon* species. It was concluded that the present high-mountain biome evolved on the low-lying plainland during a period when the environmental conditions there were similar to those of the high altitudes today. Thus the high-mountain biome is not an autochthonous relict, but is in refuge in an area to which it has retreated after its area of origin became uninhabitable due to aridification and temperature increase.

The systematic revision and cladistic analysis of the genus *Colophon* includes the descriptions of two new species, *C. barnardi* and *C. montisatris*.

The discussions are introduced by sections on speciation, environment-organism relationships and interspecific competition.

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## INTRODUCTION

The Coleoptera Department of the Transvaal Museum, Pretoria, has adopted historic biogeography as a central theme of research. During the past ten years geographic areas that are of significance in the biohistory of the subcontinent have been selected for fieldwork.

While tracing the origin of the Namib Desert biome, the west-coast area was investigated from the Namib Desert to the winter-rainfall area in the south. Simultaneously the faunal contacts of isolated indigenous forest areas in the Drakensberg and southern Cape mountain ranges were studied. All observations so far lead towards the conclusion that the roots of our primordial fauna are southern in their origin. The Gondwana origin and post-Gondwana radiation of some of our oldest faunal elements from south to north have been discussed previously (Endrödy-Younga 1978). An historic contact between the Cape and south-western biogeographic zones (Endrödy-Younga 1978) also became evident, but was this by derivation or by simultaneous evolution under distinct zonation of environmental conditions? It was clear that the next logical step was to learn more about the oldest stratum of the Cape biome, the Gondwana relicts.

As a starting point, Barnard's (1929, 1932a, 1932b) studies on the lucanid genus *Colophon* were selected. Barnard and his fellow members of the Mountain Club discovered a number of species of this genus living exclusively in high-altitude mountain habitats of the southern Cape. He compared this distribution pattern to that of the isopod crustacean genus *Phreatoicus* (Barnard 1929). In doing so, he was the first to base on evidence from the invertebrate fauna the suggestion that all the high-mountain organisms—and not only the vegetation—are members of a distinct biome of common origin, and that this habitat has historic significance.

Barnard's hypothesis (1929: 180) attributed geological ages to the inhabiting of mountains, and explained the fragmentation of populations by fragmentation of the mountains. While a time scale thus visualized is exceedingly long, it would in any case solve only a few of the problems. Nevertheless, the relict character of the high-mountain biome is still widely accepted today.

Intensive collections of invertebrates have been made at and around known habitats of *Colophon* species, in a search for phylogenetic and geographic connections between the faunal elements. This fieldwork and its evaluation are still in progress.



Fig. 1. *Colophon montisaris* sp. nov. Male in its natural environment in the Swartberg Range.

It was not my intention to revise the 'marker' genus *Colophon* until one of the species collected in 1978 proved to be undescribed (Fig. 1). As the revision progressed, the problems relating to the faunal history grew alarmingly, but the solution presented itself when the results of the cladistic analysis of the species were compared with their present-day distributions.

The derivation of the conclusions is lengthy and the time for reading is limited for everyone. The paper is therefore presented in the reductive style. Thus I start with my statements *in medias res*, with ample references to the succeeding sections, where the reasoning can be followed and checked.

#### PAST COOL TEMPERATE AND HUMID CLIMATE IN THE CAPE, AND LOWLAND ORIGIN OF THE HIGH-MOUNTAIN BIOME

Many components, plants and animals, live today exclusively in the alpine regions of the Cape mountains. As all organisms are persistent in environmental conditions to which they have adapted during their speciation (see p. 367), the present high-mountain conditions must be largely the same as they were when the component taxa evolved. There are two possible reasons for this situation: either the biota live where they have evolved (autochthonous) and the conditions in the area have not changed markedly, or the biota evolved somewhere else where the conditions were similar to those where they live now and the biota changed



geographic position due to a shift of climatic zonation. In the first case the whole biome represents a relict, and in the second it is in refuge (see p. 370).

The conclusion that the high-mountain biome has been translocated from its area of origin, which was the country of low elevation around and between the mountains, has been reached by the following sequence of hypotheses and observations.

(a) If the biome is autochthonous, a clinal type of character transformation would be expected along the Swartberg and Langeberg ranges. Dispersion and subsequent speciations could occur only along the gradients of the ranges. Under these circumstances distant isolated conspecific populations cannot occur.

(b) Conspecific populations split between mountain ranges are not known in *Colophon*, although some populations are separated by deep passes (*C. primosi*), or by hilly country, far below their present altitude (*C. stokoei*). Different species of the monophyletic genus are, however, separated from each other by extensive plains, of which the most striking example is *C. westwoodi* on Table Mountain. Distantly isolated conspecific populations are well known among plants, e.g. *Protea pruinosa* occurs on Blesberg (in the middle of the Swartberg) and in the Cedarberg. The same can also be expected in other invertebrates, as Barnard pointed out in the isopod genus *Phreatoicus* (1929: 182).

(c) The cladistic analysis of *Colophon* species (see p. 374) indicates that species of closest kinship relation might occur today in different mountain ranges. *Colophon whitei* and *C. montisatris* sp. nov. live at the eastern distribution limits of the genus in the heights of the Swartberg. Species from which they cannot be derived (*C. primosi* and *C. neli*) block their west-to-east route of mountain dispersion. Their closest kins, both in the apomorphic (*C. izardi*) and the plesiomorphic condition (*C. thunbergi* and *C. barnardi* sp. nov.), inhabit sections of the Langeberg, on the other side of the Little Karoo.

(d) The only hypothesis that resolves the problem is that the high-mountain biome evolved around the mountain ranges, where most of the evolutionary lineages have also been separated (in some cases down to the extant species). Considering the persistence of species in their native climatic conditions (see p. 367), the climate of the Little Karoo and a part of the Great Karoo (see p. 363) is expected to have been approximately as humid and as cool in the past as the alpine regions of the Cape mountains today. In order to attain these conditions in the surrounding Karoo, the regional temperature would have to drop to a level that would result in a high-altitude snow cover throughout most of the year.

Due to gradual aridification and temperature increase the low-lying country became uninhabitable, but at the same rate the climate of the mountains became hospitable. Populations of *Colophon* species and their ecological allies gradually moved to higher altitudes in the mountains. Those species that had no access to high mountains became extinct when their refuges became uninhabitable.

The ancestral *Colophon* population had ample space for dispersion, particularly when they gained access to the Little and Great Karoo. The



speciating populations could form a mosaic-type distribution on the open flat country. The dispersion-*cum*-speciation process was not necessarily along a gradient, as it would have been if it had occurred on a mountain range. Phylogenetically distant species would then be able to find refuge on the same range, e.g. from either side (see kinship of species on the Swartberg). Similarly, the distribution of conspecific populations of closely related species could split and shift towards different ranges (*Protea pruinosa* on Cedarberg and Swartberg, or *Colophon whitei* and *C. montisatris* sp. nov. on Swartberg and *C. thunbergi* and *C. izardi* on Langeberg).

(e) The role of competition as a driving force for species to occupy alien biotopes, at least in the animal kingdom, is rejected (see p. 368). Interspecific 'competition' might have a certain role in the food chain; thus the appearance of hitherto absent predators might accelerate the extinction of their prey.

#### CLIMATE AND VEGETATION OF THE PAST LOWLAND HABITATS

The concept of persistence of organisms in their native environmental conditions (see p. 367) suggests that their original requirements had to be similar to those prevailing at present in the alpine regions, i.e. considerably more humid and considerably cooler than they are now in the southern parts of the Great Karoo. The similarity of native conditions of different species is expressed clearly by the altitudes at which they were taken in the different ranges. In the Swartberg range the species occupy only the highest altitudes (approximately 2 000 m), and are absent from any lower intervening sections. In the Langeberg, however, they are less restricted to the heights of the peaks within their distribution areas (from 1 300 m up). Of these two ranges the northern (Swartberg) is the drier, with less frequent cloud cover, higher summer temperatures, and a long dry spell in summer. The relevant altitudes in both ranges (and even lower altitudes) are regularly snow covered during two to three months in winter. The lowest zone on Table Mountain that is occupied by a *Colophon* species is below 1 000 m.

Field observations (see p. 372) revealed that adults are active in any period of the summer months but appear only under optimal weather conditions. All specimens were sighted (in both Swartberg and Langeberg ranges) in the morning or afternoon hours, mostly in thick fog, and on one occasion (Langeberg) in light rain (Fig. 2). Specimens were seen in the late afternoon hours in the spreading shade of peaks in clear weather, but not during sunny noon hours as Barnard mentioned (1929: 178).

Their high humidity requirement is quite evident from the habitat data and field observations. The low temperature as a factor of native conditions is more difficult to test directly. There is, however, some circumstantial evidence to suggest that low temperature was also part of the native climate.

If high humidity was the sole requirement, *Colophon* species could inhabit the forests that are, in places, within a few kilometres of their present habitats.

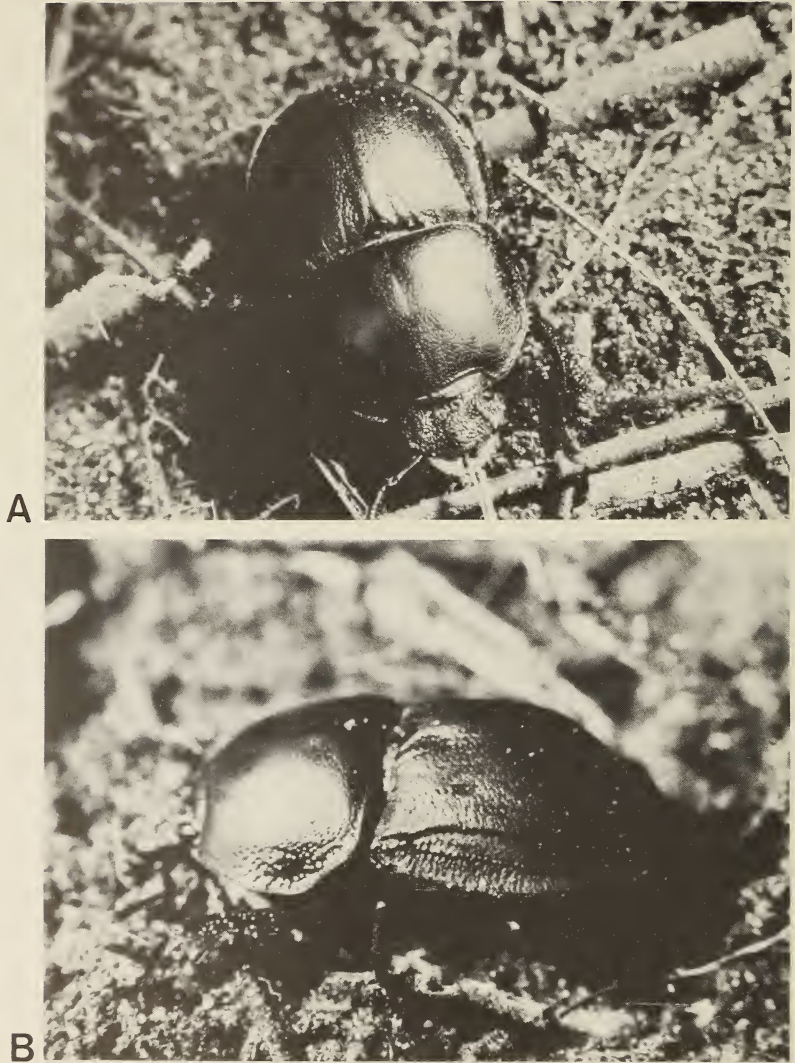


Fig. 2. A-B. *Colophon izardi* Barnard, female. The first live *Colophon* specimen photographed. A. Dorsal view. B. Lateral view.

The forest habitat, however, is alien to *Colophon* and apparently much more so than the low temperatures of humid alpine altitudes and the regular snow cover. Thus to accept low temperature, *Colophon* required little or no adaptation, i.e. deviation from its native condition.

The Northern Hemisphere glacial faunal fluctuation, as observed by Coope (1979) in the British Isles, suggests a rather strong temperature adherence of the coleopterous fauna (see p. 368).

## THE ASPECT OF ABSOLUTE TIME

The study of *Colophon* does not offer any direct evidence (see p. 377) of the time when the habitat shift from the lowland to the alpine habitats occurred. However, the *Colophon* species are strictly associated with the fynbos vegetation type, and are restricted to its stratum of alpine altitudes with the implied climatic conditions. Dated changes in the extent of the fynbos vegetation could provide such evidence.

The first evidence (to my knowledge) of lowland fynbos far outside the present distribution area was identified recently by Scholtz (1985), who found *Protea* pollen deposits at 30°22'S 18°26'E.

The climatic change accompanied by the habitat shift to the mountain heights seems to be a Plio-Pleistocene event coloured by several waves of lesser climatic fluctuations (see Brain 1981). The close kinship of isolated *Colophon* species and many known fragmented conspecific populations in other groups of organisms (see p. 362) strongly support this hypothesis. Australian researchers have come to similar conclusions with regard to their local conditions.

THE GEOGRAPHIC EXTENT OF PAST HUMID AND COOL  
TEMPERATE CLIMATE

Global climatic zonation was not of the same intensity throughout the Earth's history; it is conceivable, however, that it always had an effect on the climate of the subcontinent. It can thus be assumed that the cool temperate conditions became reduced northwards in the middle of the area.

Present distribution records of *Colophon* demarcate the area between the Great Karoo and the southern coastal flats as the area where the evolution of the genus took place. The unrelated western species (*C. primosi*, *C. neli*) of the Swartberg range, blocking the dispersion range of the two apomorphic species (*C. whitei* and *C. montisatris* sp. nov.) (see p. 377 and Fig. 1), suggest that the former two species might have reached their present positions from the Great Karoo. We do not know, however, how far to the north of the Great Karoo was originally inhabited by *Colophon*. Recent visits to some heights of the Witteberg and Cedarberg ranges yielded no trace of *Colophon*, although these ranges have well-developed fynbos vegetation. The ancestral stock of *Colophon* was associated with the extremely cool and humid type of flatland fynbos in the south-western corner of the Cape, and did not necessarily disperse with it into its ecologically marginal northern types. Nevertheless, it is possible that some of its populations shifted northwards when aridification first commenced in the central Karoo.

Past occupation of the southern coastal plains is uncertain. The ancestral species of the genus were certainly already apterous, non-wood-boring (in the larval stage), and likely to be associated with open (low and scattered canopy) fynbos-type vegetation. Areas that were taken over by dense forest vegetation in more humid periods have thus been excluded from the past distribution of *Colophon*.



## OBSERVATIONS AND BACKGROUND STUDIES

In the present paper a monophyletic group of stag beetles is studied. The relationships between the 14 recognized species were established by cladistic analysis. The cladogram thus obtained is compared with the present distribution of the species and conclusions are drawn as to what environmental conditions might have facilitated the dispersion of populations to reach their present loci.

Before entering the discussion the premises of this study need to be outlined. Some of them are widely accepted and sufficiently described; others, however, have been neglected or even sharply disputed as valid forces of evolution.

## SPECIATION

The genetic process of evolution will not be discussed, but rather the status and fate of populations that can or cannot lead to a speciation event. Phyletic gradualism, which proposes sympatric speciation and an accumulation of imperceptible changes as a means of speciation, is rejected (Mayr 1942; critique in Hennig 1966; Paterson 1978). The accepted alternative pattern is that of punctuated equilibria (Hennig 1966; Eldredge & Gould 1972; Paterson 1978). According to this pattern, speciation is an event and not a continuous process; the species are real entities and not subjective fabrications of the observer when he slices convenient sections of the phenetic continua. The species retain their genetic identities for a long period of time relative to the short period of the speciation event leading to them. They do not transform in themselves, but cease to exist when the last population representing them becomes extinct in time. Their genetic continuity is manifested in their daughter species (if formed), or their lineages become extinct with the last surviving species. The physical precondition of any speciation event is the accidental formation of population fragments. Such fragments might speciate (should they survive) if their populations are sufficiently small, the environmental conditions of their new habitats are sufficiently different, and they remain in isolation from other populations for a sufficiently long period of time. It is evident that these rather independent conditions would seldom coincide. Thus the frequency of speciation events will depend both on the genetic constitution of the species involved and on the lability of climatic conditions, aggravated or eliminated by the other components of the environment. The same environmental changes would affect populations of different species (with respect to 'isolation' and speciation) quite differently. This observation emphasizes that 'isolation' hardly depends on the magnitude of the environmental differences, but primarily on the genetically determined reaction of the organism (see also p. 367).

## CLADISTIC METHOD OF TRACING KINSHIP

It is claimed that phenetic similarity, if evaluated correctly, reflects the degree of kinship. The theory formulated by Hennig (1966) has an ever-growing literature where the methodology of cladistic analysis is adequately described.

Here only some of the basic premises of the cladistic theorem will be recalled. The analysis is based on the occurrence of the same derived characters (synapomorphies) in two or more species. It means that those species that show the highest numbers of synapomorphies, i.e. the latest acquired stages of the transformation of the phenotypic characters, have the closest kinship. This also implies that the weighting of characters is not a part of the evaluation. Actually, the common occurrence of a normally infraspecific character in the phenetic spectrum of two species would indicate the closest, sister-species relationship (Endrödy-Younga 1981).

#### THE ORGANISM—ENVIRONMENT RELATIONSHIP

At every single speciation event a set of adaptive characters becomes fixed within the genetic spectrum of a newly established species. The ultimate 'reason' for speciation is to provide the forthcoming generations with a set of inherited characters that enables the individuals to cope with the environmental conditions into which they are born, without the necessity of ever repeating adaptation.

For any organism to survive it is absolutely essential to possess a basic set of adaptations as an inherited genetic asset to cope with the 'normal' or average fluctuations of its native habitat. Thus its apparently limited adaptive capacity is left open to cope with changes within its environment. If this were not the case, any new-born land organism, even today, would first have to adapt to conditions on land, leaving little chance ever to enter complex environmental situations. Terrestrial life would still be struggling for survival along the coastlines.

If speciation is a complex genetic response to a new set of environmental conditions into which the new population fragment was forced, it is easy to understand that the speciated population will be conservative in its further habitat selection; in other words it will stick to its native habitat.

Thus no population will enter a habitat alien to its native type, a habitat for which it is not equipped in its adaptation complex. A population might, however, be stranded in such a habitat by accident; thus it is much rather a 'shipwreck' than a 'colonizer' population. For example, parts of populations of a forest-dwelling species will not endeavour to enter and colonize the surrounding savannah habitats, but may be 'shipwrecked' on them if the forest, which the species was inhabiting, first became fragmented, then gradually disappeared due to climatic changes. The classical island 'colonizers' (e.g. of Hawaii) are in this sense no less 'shipwrecks'. They all reach the islands accidentally and have to encounter the new situation with their various capacities for adaptation.

It is evident that the balance between the magnitude of difference under the native and the new environmental conditions on the one hand, and the adaptive capacity of the population involved on the other, will determine whether the 'shipwreck' population will be able to adapt and survive, or will become extinct. The magnitude of adaptive capacity is a specific character, expressed in habitat utilization with specialists and generalists as the two extremes.

The ever-changing environment is a permanent stress on the organic world that might be countered in two different ways. Either the tolerance to such changes increases infinitely in the organism, resulting in a few infinitely flexible forms, or parts of the organic world specialize to one or other type of condition, resulting in increasing diversity. Apparently an infinite flexibility could not be attained and the mechanism to adapt to particular conditions has developed. The species with its genetically fixed adaptation complex is a foothold (and apparently the only one) to a further change that the environment might provoke.

The inherited adaptation asset is the tool of survival for the individual in its native environment, and the fixation of new adaptations through speciation is the mechanism of the biota to survive the stress of the ever-changing environment.

The key statement to the present theory is specific habitat conservatism (see above). Clear evidence for this statement was provided by Coope (1979), who studied the coleopterous fauna of peat accumulations deposited through a number of successive glacial and interglacial periods. It was found that practically identical assemblages of species disappeared and reappeared with the fluctuations of the glacial periods. At present, in the middle of an interglacial, most of the species known from the glacial peat deposits in England are known to be extant in their cool-climate refuges as far away as in central Asia. There is no evidence of phenetic transformation according to the phyletic model of speciation, and it is reasonable to expect that the same species will reappear again if glaciation were to recur.

It can be concluded that in speciation a new, adjusted habitat preference will be attained along with other simultaneously fixed characters. The species will stick to its acquired habitat, as its whole set of adaptations refers to that particular habitat and not to any other. As a result the species will readily extend its distribution area if its habitat is expanding spatially (due to climatic change), but its distribution will again contract if the climatic trend is reversed.

#### COMPETITION

Interspecific competition as a driving force of evolution in the animal kingdom is emphatically rejected.

The term competition was introduced in biology for situations where individuals exert pressure on one another in order to obtain more (enough) of their environmental necessities. These necessities range from food and breeding ground to the most general term of 'Lebensraum'. It is claimed that by this action entire populations might be driven into other, less advantageous habitats. It is also often implied that such enforced habitat changes, leading to speciation, represent an important factor of evolution. Without trying to comment on rare and isolated cases (such as sessile benthonic animals) of habitat change for this reason and possible speciation resulting from it, I believe that the course of evolution rests on the balance of the organism-environment relation, as discussed before. In other words, evolution does not 'benefit' from competition, and least of all from that within biota of the same trophic level.



What does interspecific competition imply? It is evident that those individuals whose demands in the 'Lebensraum' are the most similar would be in the fiercest competition against each other. This is undoubtedly the case between conspecific individuals, which share characters including that of identical habitat requirement. Thus it is only logical that competition should act most strongly within the species rather than between species.

Undoubtedly, there is interspecific competition in the plant kingdom, e.g. if a dense-canopy tree grows in the midst of a carpet of sun-loving plants, it will successfully compete with them because neither can change position in order to move out of the disadvantageous sphere of influence of the other. The outcome will be that some of the badly affected individuals would die in the shaded area. But assume that in time the entire deep-soil, well-irrigated flat area is taken over by the forest; would the herbaceous plants of this habitat gradually move onto the shallow soil of the over-drained hillside?

It is certain that one of the advantages achieved in the animal kingdom by the 'invention' of locomotion was that animals capable of it can 'step aside' if another individual enters their sphere of interest.

The concept of interspecific competition in zoology was certainly borrowed from botany. All sorts of distribution patterns, unclarified situations of balance in ecosystems, and behavioural differences in cohabiting species were simply explained as results of competition. To illustrate the above, the Namib Desert biome may be cited as an example.

It is found that congeneric species have slightly different habitat preferences on the dunes; it could be claimed that interspecific competition keeps them apart. I believe that the native microhabitat of the different species is reflected in their present habitat selection. The allopatric speciation areas of many species involved is proven (Endrödy-Younga 1982). The same applies to the high-mountain biome under discussion.

In the desert biome several tenebrionid species might live together in the same hummock or on the same dune; some of them are diurnal, others nocturnal. It has been claimed that the activity pattern of the different species has shifted apart due to competition. The time pattern is, however, a generic or more often a tribal character (Eurychorini and Caenocrypticini are nocturnal, Zophosini and Adesmiini diurnal, in their sometimes continent-wide distribution area). Thus the activity pattern is a much older genetic character of the evolutionary lineages than the co-habitation of a few of their extant representatives that might be thought to compete.

It is claimed in this paper that competition is not a driving force of evolution or dispersion of biota. Unusual pressure on an ecosystem by the importation of new species as a result of various causes, ranging from human importation to continental collision, might be expected. This might drastically alter the composition of the fauna (e.g. Marsupialia in South America), but mainly in the direction of extinctions. We have little evidence that rapid speciation has ever started in an indigenous fauna owing to the arrival of successfully competing biota.

Competition in the food chain could be another possibility. It can be claimed that the prey species move out into an alien habitat to avoid the pressure of predator(s). I have not heard, however, of antelopes vacating the savannah and moving into the forest due to the activity of lions. The competition between predator species for a limited quantity of prey could still be a possibility. In this case, however, conspecific individuals have identical habitat and prey selection, but members of other predator species do not. It would be more likely that the excess population of the predator that upset the balance would be eliminated than that another prey species would be badly affected. Thus neither the difference in habits nor habitat selection between predator species is due to competition. Cheetahs have similar habits and habitats throughout their distribution areas and these are different from those of lions, whether or not they occur together. Probably the best support for this is provided by examples of biological control; pests and predators live together in an oscillating equilibrium without either becoming extinct. Even human influence can tip the balance only if new predators or parasites are introduced, but not by the propagation of the indigenous ones.

#### WHEN IS A BIOME A RELICT, AND WHEN IS IT IN REFUGE?

The term relict is used equally for biota and for habitats if they are isolated remnants of earlier periods of larger distributions and habitat continua. Thus it has a clear implication in time. Does the term relict, however, mean unequivocally that biota were left behind *in situ* where they evolved and that the relict habitat of today formed a part of the earlier continuum? In other words, has the term relict a similarly clear spatial implication?

It has been seen (p. 367) that species persist in environmental conditions that were associated with their speciation; in other words, species are conservative in their habitat selection. In an ever-changing environment the biota are forced to follow the spatial shifting of climatic zonation. Parts of populations might be left behind *in situ* where conditions are persistent: e.g. gallery forests remaining from a forest belt during an arid period. Such a gallery forest is, in time and space, a relict habitat and its biota might consist largely of relict populations, i.e. relicts in the sense of time and space.

Climate zones might, however, together with their persistent biota, sweep through areas that were previously under the regime of different climatic zones. Under particular conditions such a moving biome might be stranded in a geographic position distant from its original position, where it no longer exists. Such a habitat and its biota are relicts in the temporal sense, but not in the spatial sense. They were left behind from an earlier epoch, but not *in situ*. In other words, these biota are not autochthonous.

The term for such translocated relict habitats is refuge habitat or *refugium*, and applies equally to the biota characterizing them. There is terminological difficulty in describing in one word the biota or species in a refuge habitat, and this might have been the reason why they are simply called 'relicts' without distinction.

It will be shown in the following section that the distinction between relict and refuge habitats and their biome is crucial to the understanding of the history of an area where relicts, in the broad sense, occur. It will also be shown that the biota of the Cape high mountains are in refuge, and do not represent a relict in the spatial sense.

#### OBSERVATIONS ON LIVE SPECIMENS

Very little is known of the biology of the *Colophon* species, and observations are restricted to a few live specimens in nature (Fig. 3) and in captivity.

In October 1977 several high-mountain areas were visited, both in the Swartberg and Langeberg ranges. Although on that occasion no live specimens were seen, it was possible to mark two sites for further studies. The indications of the prospective sites (one in each range) were fragments of dismembered specimens of *Colophon* beetles found in debris and under stones. Large numbers of ground-traps with preservative were set in both areas but they yielded no specimens of *Colophon*, although later several specimens were sighted within a few metres of operating traps. It was concluded that none of the baits used, including fermenting banana, had any attraction for these species. During three subsequent years the two selected sites were visited five times. On three occasions live specimens were seen and observed; each time some of the specimens were taken live to Pretoria, where they were observed for periods of up to 84 days. Our scanty knowledge comes from these field and laboratory observations of live specimens.



Fig. 3. *Colophon izardi* Barnard, male, in its natural environment in the Langeberg Range.



The native habitat in terms of habitat diversity is markedly different for the two species observed. The habitat of the Swartberg species, *Colophon montisatris* sp. nov., was demarcated in a tiny area of about 400 m horizontally and 20 m vertically. Outside this area not even fragments of specimens could be found, despite the fact that no obvious change in any of the environmental conditions could be seen. However, the Langeberg species, *C. izardi*, was found at sites 8 km apart and differing in altitude by about 400 m. The same species is known from five additional localities at increasing distances from the observation area. Although a detailed evaluation of environmental differences between the altitude extremes is not available, the differences in other parameters, such as soils, vegetation, exposure, etc., seemed to be considerable between the high open crest and the broad valley between two crests.

The striking difference between the *Colophon* habitats on the two mountain ranges is obviously due to their general climatic situation. The Swartberg population appears to occupy the last remnant of a habitat still acceptable to it, and it is likely that it is on the verge of natural extinction unless the regional climate soon turns more humid and cooler, thus extending spatially its native habitat. This is a classical 'bottle-neck' situation, providing selective pressure for a trapped population to speciate. Indeed, the climate of the Swartberg is drier and warmer compared to the Langeberg; rain and mist are less regular in the summer months. The same altitudes at which *Colophon* lives in the Langeberg (down to 1 400–1 600 m) are very dry after December in the Swartberg, where the peak of activity of beetles in general has already passed. In the Langeberg the mist zone is lower, and although dry spells might occur there too, the climate is more humid throughout the summer. *Colophon* specimens were seen live in both localities in February too, but with the described difference in their altitude range.

I am of the opinion that *Colophon* species in general have a much less-restricted seasonality of adult activity than Barnard (1929: 178) suggested. Barnard recorded, for example, *C. izardi* in October and November, and I have seen them in December and February; thus the adult activity period covers the whole summer at that altitude. The habitats might often be covered in snow until August or September, persisting from March or April. The surface activity of adults is likely to be triggered by optimal conditions at any time during the summer and is not restricted to any particular period of it. The pattern of scattered days of surface activity of an individual is likely to last through several years. This opinion might be supported by specimens, particularly females, that have the anterior tibiae strongly eroded. This degree of wear also occurs in Tenebrionidae, but only in species that could be kept in captivity for many years.

According to observations *Colophon* species are decidedly diurnal in activity. On all occasions when live specimens were sighted 'observation shifts' were organized, in order to scan the area with powerful lamps throughout the night. However, not a single *Colophon* was sighted, although hundreds of other Coleoptera were collected. Observation on live captive specimens confirms the diurnal activity.

The optimal weather conditions for surface activity can also be defined. Five specimens of *Colophon montisatris* sp. nov. were sighted within an hour, in thick fog after sunset (Swartberg, February 1979). One specimen of *C. izardi* was seen (Langeberg, December 1977—the very first live specimen) at about 16h00 in drizzling rain and biting cold wind. All other specimens were seen in late afternoon hours, often after sunset but before dark. Barnard (1929: 178) mentions 06h00–08h00 as the collecting hours of most of his specimens, and records as exceptional two specimens that were collected 'at midday in hot sun, though amongst low vegetation'. Nevertheless, it is clear that these beetles prefer the cool and humid periods of summer days, when their refuge habitat is not under snow. Again this is an indication of the climatic conditions of their lowland native habitat.



Fig. 4. *Colophon montisatris* sp. nov., male. This specimen's activity was observed for over an hour.

Circumstantial evidence suggests that *Colophon* species have a subterranean life, where their larvae feed on the roots of plants. On two occasions males of two species (*C. izardi* and *C. montisatris* sp. nov.) were observed undisturbed for over an hour. I had hoped that they would lead me to a female (that of *C. montisatris* sp. nov. was not yet known at that time), or would chew on something, dig in, or withdraw to their own burrow when it became dark; they did absolutely nothing. Their slow movement seemed to be entirely undirected and aimless and revealed nothing at all of their habits (Fig. 4). Specimens in captivity did not accept any food provided for them; this included a range of plants from their habitat, obtained from the Botanical Gardens, Pretoria. None of the captive specimens were observed to feed (seven specimens, over periods ranging from 15 to 84 days) unless on the vegetation debris that was richly supplied in the soils brought with them.

CLADISTIC ANALYSIS OF THE *COLOPHON* SPECIES

As will be explained (p. 381), the higher classification of this group can only be clarified in conjunction with a comprehensive revision of the whole family. At this stage we have to be satisfied with the recognition of the genus as a monophyletic group. The general structure displayed by all 14 species suggests that this group is not only monophyletic but forms one single genus.

The 14 species form two distinct groups indicated by the symmetry of the aedeagus and the single correlated character found, i.e. the level of the clypeal margin (see p. 385). However, separate genera could not be allocated to these species groups, as one of them—comprising the plesiomorph species—apparently does not possess any apomorphic character states among the numerous characters studied.

The two species groups are interpreted as two distinct evolutionary lineages within the genus. The first group, comprising the plesiomorph species, is a result

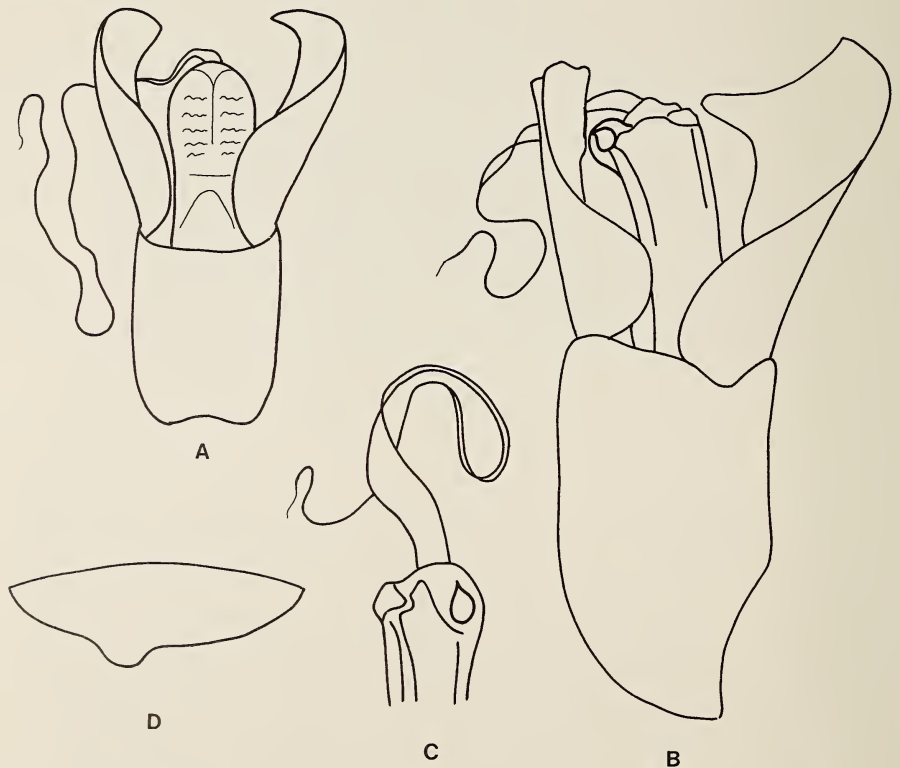


Fig. 5. Lineage characters in the genus *Colophon*. A. Symmetrical aedeagus in the plesiomorphic lineage, as in *C. haughtoni* Barnard. B. Asymmetrical aedeagus in the apomorphic lineage, as in *C. primosi* Barnard. C. Apical portion of penis with the non-retractable inner sack as in *C. primosi* Barnard. D. Asymmetrical anal sternite in *C. montisatris* sp. nov., typical for the males of the apomorphic lineage.



of the first cleavage and possesses as apomorphies only those characters that ensure the generic position of *Colophon* itself. The generic apomorphies can only be recognized through out-group comparison, but at this stage we do not know what should be considered as an out-group for *Colophon*. However, the existence of true generic-level apomorphies (applicable to all species included) is confidently postulated. The phenetic distinctness of the Cape stag beetles proves their integrity at least at generic level. The problem is indeed to find a relative to them at all.

The two evolutionary lineages represented by the two species groups can be characterized as follows. *Plesiomorphic lineage*—Aedeagus of symmetrical type, parameres very nearly identical or symmetrical; anal sternite evenly rounded posteriorly. Penis feebly sclerotized with distinct transverse undulation on the shaft (Fig. 5A). Clypeus meets labrum on an even level. *Apomorphic lineage*—Aedeagus of asymmetrical type, right paramere strongly dilated towards apex and forms a sharp hook at its inner margin, left paramere slender and without inner hook (Fig. 5B). Anal sternite correspondingly asymmetrical at its posterior margin, emarginate to the right of its median axis so as to provide space for the enlarged right paramere at ejection (Fig. 5D). Penis well sclerotized with very distinct and asymmetrical apical portion (Fig. 5C). Anterior margin of clypeus raised above the level of labrum at their suture.

The symmetrical structure of the penis is a key and irrefutable character to denote the plesiomorphic position in the lineage of species that share this character.

The above group characters are not used in the following analysis, which is based on the transformation series given below. The analysis of each lineage is carried out separately. Often the same characters are used, and are sometimes represented in both transformation series in the manner: absence to presence (plesiomorph group), presence to distortion (apomorph group).

#### *Transformation series in the plesiomorphic lineage*

1. Apico-ventral process of anterior tibia small to *large*.
2. A longitudinal crest at the ventral side of anterior tibia more or less uniform and moderate over whole length to *sharply raised* in its basal section.
3. Apico-ventral process of anterior tibia in central position to *shifted to inner margin*.
4. Dorsal process of mandible absent to *present*.
5. Ventral process of mandible concealed to *free standing* and prominent.
6. Lateral margin of pronotum evenly curved along whole length to deeply *emarginate* before reaching posterior lateral angle.
7. Anterior margin of pronotum immarginate at its median section to *continuously marginate*.
8. Gula flat along whole length to *sharply concave* (lateral view).
9. Prosternal apophysis simple to forming a *sharp tubercle* at its caudal (intercoxal) end.

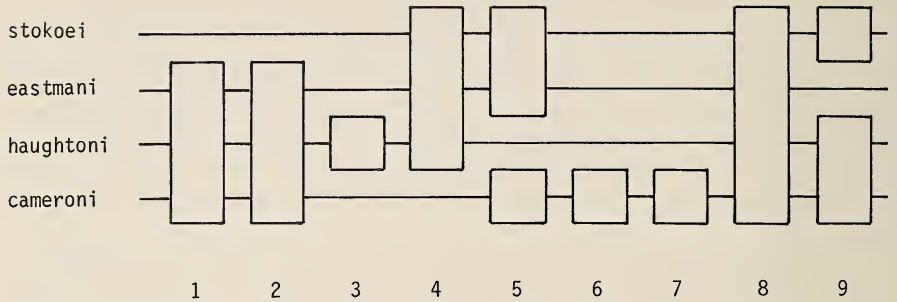


Fig. 6. Tabulated record of apomorphies in the plesiomorphic lineage of the genus *Colophon*. Figures below the histograms refer to characters evaluated in the text.

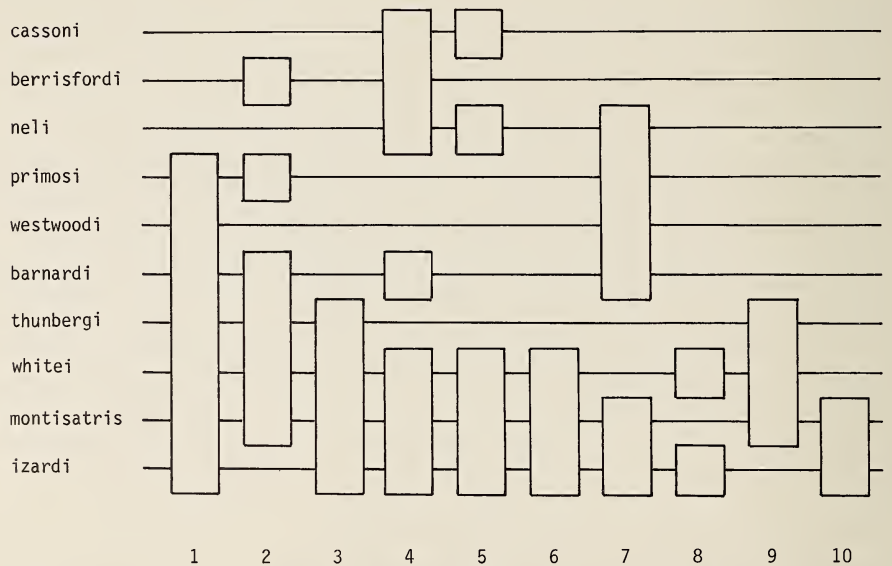


Fig. 7. Tabulated record of apomorphies in the apomorphic lineage of the genus *Colophon*. Figures below the histograms refer to the characters evaluated in the text.

*Transformation series in the apomorphic lineage*

1. Apico-ventral process of anterior tibia present, reducing to *absent*.
2. Inner angle of anterior tibia rounded to forming a *prominent process*.
3. Anterior tibia straight to *bent inward*.
4. Longitudinal ventral elevation of anterior tibia flat and rounded to *sharply crested*.
5. Lateral margin of anterior tibia with several spaced teeth, through trifid to *bifid* apical portion.
6. Anterior tibia evenly curved at external margin to a deep *U-shaped emargination* in pre-apical position.

7. Dorsal process of mandible present to *absent*.
8. Ventral process of mandible in basal, to *median* or *apical* position.
9. Lateral margin of pronotum moderately to *sharply* and *deeply emarginate* posteriorly.
10. Gena evenly rounded behind eye to a distinct *postgenal protuberance*.



Fig. 8. Simple female mandibular structure in *Colophon westwoodi* Gray. The mandibles are very similar in females of all *Colophon* species.

Where applicable, the very uniform display of character states in females was used for out-group comparison in deciding on the polarity of the transformation series. Females generally, but notably in Lucanidae, are more conservative in phenetic changes and thus can be considered in most characters to be close to a hypothetical ancestor (Figs 8, 14A). In some other characters, stages uniformly displayed by the symmetrical-aedeagus lineage, were considered as plesiomorphic states in the genus, e.g. the presence of an apico-ventral process of the anterior tibia and the presence of a dorsal process of the mandible.

The synapomorphies, as displayed in the plesiomorphic and in the apomorphic lineages of species respectively, are shown in Figures 6 and 7. From these data a cladogram was constructed (Fig. 9). On the branches the numbers of synapomorphies are marked in squares and the numbers of autapomorphies in circles, indicating the position of terminal species.

#### THE PRESENT-DAY DISTRIBUTION OF *COLOPHON* SPECIES COMPARED WITH THEIR EVOLUTION

It is assumed that *Colophon*, as a monophyletic genus, had a single ancestral species. From this ancestral population, by the repeated speciation of marginal population fragments, an increasing number of species has evolved. In a slow-moving, wingless and terrestrial type of organism such as *Colophon*, the process of dispersion must have been slow and the chances of population fragmentation,



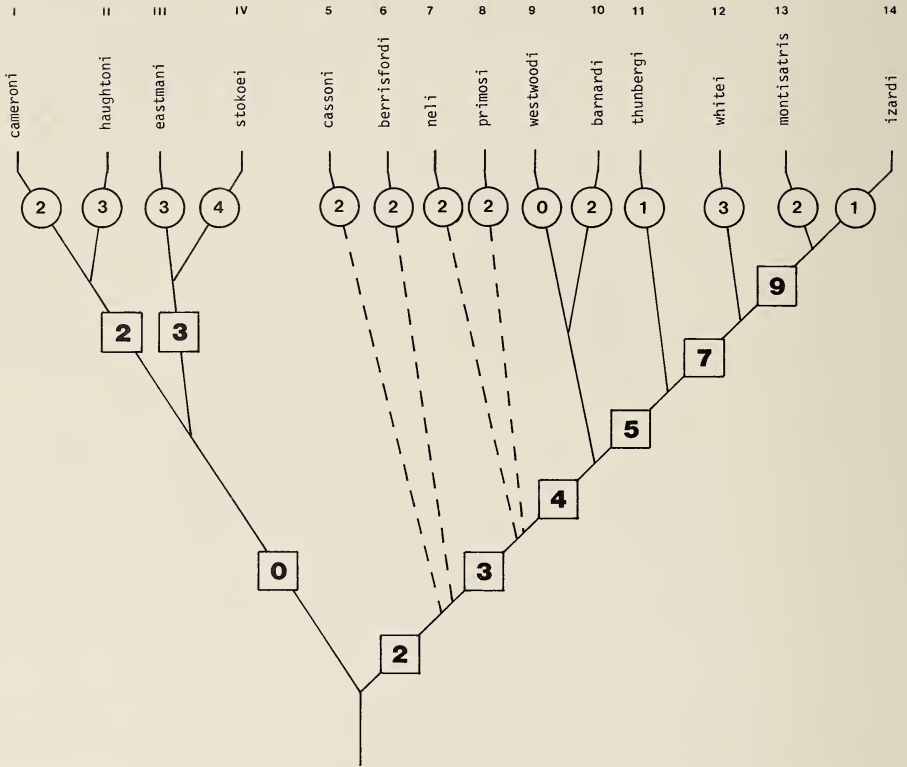


Fig. 9. Cladogram of *Colophon* species. Figures in squares show the numbers of synapomorphies found; figures in circles show the numbers of autapomorphies found in the individual species.

affecting spatially advanced marginal populations, rather good. If the character transformations in species of such a group of apterous organisms are studied along a geographical gradient, a clinal pattern will usually be found. This is only to be expected as the phenetic reflection of a chain of subsequently forming daughter species. Similar observations have also been made on apterous tenebrionids (Endrödy-Younga 1982).

The assumption that *Colophon* and its entire high-mountain biome is an *in situ* relict of past climatic epochs should be dramatically proved by the phenetic cline of *Colophon* species along the mountain ranges where they live. It would be expected that consecutive east-west sections of the Swartberg and Langeberg ranges should be occupied by species of closest kinship in the sequence of their specific character transformations.

However, the actual situation is very different from that expected. The plesiomorph group of species occupies the mountain ranges in the south-western corner of the area (Fig. 10). Most of the apomorphic species occupy the east-west ranging Swartberg and Langeberg mountains, but one (*C. westwoodi*) lives



Fig. 10. Hypothetical dispersion and present-day distribution of the *Colophon* species. Roman figures represent the species of the plesiomorphic lineage, arabic figures the species of the apomorphic lineage (see Fig. 9 for names).

on Table Mountain, where it is isolated at the western extremity of the mountain groups occupied exclusively by the plesiomorph species.

Similarly, the three terminal apomorphic species of the apomorphic species group are separated at the east end of the major mountain ranges: *C. whitei* and *C. montisatris* sp. nov. on the Swartberg and *C. izardi* on the Langeberg, with the arid Little Karoo between them.

Thus the dispersion and speciation of the *Colophon* stock could not have occurred on and along the mountain ranges but only on the lowland situated around the mountains. At the end of the humid and cool temperate climatic period, when the presently inhabited altitudes of the mountains were under snow most of the year, an intricate mosaic pattern of *Colophon* species inhabited the low-altitude country. Because of the gradual changes towards a dry and hot summer, the populations withdrew to the nearest mountains where they could persist under their native conditions. It is likely that several species retreated into areas that could provide only temporary shelter. Populations that became stranded in hilly country of insufficiently high altitudes could not survive during continuing aridification.

The phylogenetic position of *Colophon primosi* and *C. neli* raises further problems. They belong undoubtedly to the apomorphic species group of the genus; however, they cannot be derived from the same ancestral stock as all other species of this group. There is a strong indication that the dispersion and speciation of the *C. whitei*-*C. izardi* lineage proceeded eastwards between the main mountain ranges. It is unlikely, however, that the ancestry of *C. primosi* and also of *C. neli* followed the same route. It is conceivable that the ancestral territories of those latter lineages occupied sections of the southern Karoo, north of the Swartberg range. The same geographical situation can also be the reason why only those two species have survived whereas their closest relatives, having no access to nearby mountains for retreat, became extinct.

## SYSTEMATIC REVISION OF THE GENUS *COLOPHON*

### THE HISTORY OF STUDIES

The first *Colophon* specimens must have been collected around the turn of the eighteenth and nineteenth centuries by unknown travellers. The genus, with its first known species, *C. westwoodi*, was described by Gray in 1832; locality, date or collector of the type-specimen (in the British Museum (Natural History), London) are not known. A second, similarly old specimen in the Hope Museum, examined by Parry in 1870, bears no information regarding its origin, but was already labelled as a 'type' in Parry's time. Gray (1832) knew, however, only of one male.

The second species, *C. thunbergi*, described by Westwood (1855), is dedicated to the notable traveller and naturalist C. P. Thunberg, who visited the western Cape in the 1790s. There is no evidence that he actually collected the specimen in question, but a passage in his diary (1793) coincides with the locality



of a specimen of *C. thunbergi* in Oberthur's collection (Muséum national d'Histoire naturelle, Paris), referring to the Swellendam section of the Langeberg range. These hints led Barnard to the discovery of a population of this controversial species at the Zuurbrak Peak in 1932 (Barnard 1932*b*).

Dr K. H. Barnard revived interest in these curious beetles. As a curator, and after Péringuey, the director of the South African Museum, Cape Town, he was not only a keen student of aquatic zoology but also a devoted mountaineer. It is only to be expected that the curious high-mountain dwellers would not long evade his interest. As far as can be ascertained, the first specimens of *Colophon* collected by Barnard were those found in 1916 in the Hottentots Holland Mountains. They proved to be different from the two known species and were described as *C. stokoei* Barnard, 1929. The second record came from Dr S. Haughton, who collected a single male of yet another unknown species in the Matroosberge in 1917—*C. haughtoni* Barnard, 1929, dedicated to its collector. Thus encouraged, Barnard's mountaineering colleagues paid attention to these curious beetles during their excursions, and their efforts are reflected in Barnard's dedications of new species collected. All nine of Barnard's species are named after members of the Mountain Club of South Africa. (I have completed the eminent list by naming one of the new species after the former President of the Club, Dr K. H. Barnard.)

In his first paper on *Colophon*, Barnard (1929) described five new species: *C. stokoei*, *C. haughtoni*, *C. cameroni*, *C. izardi* and *C. primosi*, and made the first character evaluation in the genus, pointing out the main specific characters of the male mandibles, anterior tibiae, and aedeagi. Studying the aedeagi, he first discovered that the taxonomic position of the genus under the subfamily Lampriminae is, at least, doubtful.

A plate with photographs of all species of *Colophon*, including those to be published in a forthcoming scientific paper, was published in a popular article (Barnard 1932*a*). Although the names to be used accompanied the photographs, this article cannot be considered as the place of publication (see *International Code of Zoological Nomenclature 1964*: Article 12). The proposed names became available in a subsequently published scientific paper (Barnard 1932*b*), where descriptions of *C. neli*, *C. whitei*, *C. cassoni*, *C. berrisfordi* and *C. eastmani* were given.

#### THE POSITION OF THE GENUS *COLOPHON* IN LUCANIDAE

The genus *Colophon* was until very recently associated with Southern Hemisphere subfamilies of the Lucanidae. McLeay (1819) recognized the subfamilies Chiasognathinae and Lampriminae as separate subfamilies. Following this classification, Didier & Séguy (1953) placed *Colophon* under Lampriminae. The same classification was maintained by Landin (1955) and Brinck (1956). For a long period of time these two subfamilies (both Southern Hemisphere) were combined under the name Chiasognathinae, and *Colophon* was considered a member of it (Parry 1864; Handlirsch 1908; Van Roon 1910; Jeannel 1942). Thus the actual affiliation of the genus has not changed.

Lacordaire (1856), who recognized Chiasognathinae and Lampriminae, placed *Colophon* under the subfamily Lucaninae, or '*lucanides vrais*'. All classifications mentioned so far were based on differently evaluated external characters, in particular those of males that are strongly subjected to secondary sexual character transformations.

The first author to examine the male genitalia of *Colophon* species was Barnard (1929), who was by no means a specialist of Lucanidae. Nevertheless he, referring to Sharp & Muir (1912), observed that these genitalia are distinctly more like the Lucaninae than the Lampriminae-type, and shed the first doubt on the association of this South African genus with the Lampriminae. His noteworthy discovery was disregarded by several subsequent authors.

In 1960 Holloway published her study on a wide range of species of the family Lucanidae comparing, among other characters, the structures of male genitalia. She categorically excluded *Colophon* from Lampriminae, and placed the genus under Lucaninae as Lacordaire (1856) and Barnard (1929) had done, although on a more intuitive basis.

Being concerned with the relationship and origin of the genus *Colophon*, I have repeated Holloway's study on less extensive, but representative, material from South America, Africa and Australia, including species classified under the subfamilies Chiasognathinae, Lampriminae and Lucaninae. I agree that according to Holloway's (1960) classification *Colophon* does not belong to either of the Southern Hemisphere subfamilies, but to the cosmopolitan Lucaninae. Nevertheless, the problems of relationship and origin remain unresolved. It became evident that there is no evolutionary link between *Colophon* and the other, old-world stock genera of African Lucanidae. Thus, although *Colophon* belongs to the subfamily Lucaninae, it seems not to be derived from its African old-world lineages, nor could the latter be derived from the stock of *Colophon*. Although no conclusive studies were made in this direction, some of the Southern Hemisphere genera of the subfamily Lucaninae (such as *Pholidotus* McLeay in Brazil, and *Rhyssonotus* in Australia) seem to be more closely related to *Colophon* than any of the African genera.

Thus the Gondwana origin of *Colophon* can be maintained under its classification in Lucaninae, but the problems in the evolution of the subfamily are compounded. Holloway (1960) envisaged the necessity of further subdivision of the subfamily to resolve diversity problems. Such a study might also clarify the problems surrounding origin, evolution and dispersion within the group.

#### MATERIAL EXAMINED

In the course of the present study nearly all *Colophon* specimens known to be deposited in collections were re-examined. In all 136 complete specimens and numerous fragments were seen, some of the latter being listed below under primary and secondary types. The material included four primary and 38 secondary type specimens, 46 further specimens and numerous fragments from the South African Museum, Cape Town; eight primary and 18 secondary type

specimens and eight further specimens from the British Museum (Natural History), London; the type specimen of *C. thunbergi* from Oxford; and one primary and 10 secondary type specimens and 11 further specimens and fragments in the collection of the Transvaal Museum, Pretoria. By kind courtesy of the South African Museum, some of the duplicates could be deposited in the Transvaal Museum, Pretoria.

The value of fragments, which are more frequently found than intact or live specimens, was fortunately already realized by Barnard. Some fragments, such as male heads and anterior tibiae, are perfectly characteristic of the species they represent. Barnard had already made use of such fragments in his character evaluations and listed them in his species descriptions. Indeed, in several instances the single, or few, intact specimens alone would not permit conclusive recognition of specific characters and individual variations. In this paper more importance than usual is given to fragments; where appropriate they are designated as paralectotypes and have been marked accordingly.

In listing material examined the locality data have been taken from the actual specimens labels, hence various inconsistencies in spelling, etc. Any additional information added is placed within square brackets.

#### KEY TO *COLOPHON* MALES

- 1 (8) Edge of clypeus in flush with labrum. Aedeagus of symmetrical type, left and right parameres closely similar. Penis less sclerotized with distinct transverse undulation, apical portion symmetrical (Fig. 5A). Apical sternite symmetrical at apical margin.
- 2 (3) Mentum with sharply raised anterior portion forming one or two (bilateral) rounded elevations or a deep acuminate anterior surface; sickle-shaped mandibles with ventral process at base only (Fig. 17A). Anterior tibia emarginate before apico-lateral dilation (Fig. 20C). 21–27 mm. Western Cape mountains . . . . . *C. stokoei* Barnard
- 3 (2) Mentum flat or moderately and evenly convex.
- 4 (5) Apex of mandible and pre-median dorsal process connected by a flattened shiny surface (Fig. 11B). Ventral process of mandible broadly obtuse-angled. Prosternal apophysis without any process on posterior portion. (Anterior margin of pronotum not furcate-marginate.) Anterior tibia slightly and evenly curved and dilated (Fig. 14D); apico-ventral process extremely large, cylindrical and perpendicular to tibia. 20–23 mm. Western Cape mountains . . . . . *C. haughtoni* Barnard
- 5 (4) Dorsal process of mandibles more or less cylindrical, not forming a flat inner surface; position more or less postmedian.
- 6 (7) Ventral process of mandible well developed and situated in basal position. It is flat, acute-angled, without forward-pointing cylindrical process. Dorsal process in median position, apex symmetrically truncate (Fig. 11A). Anterior tibia evenly but somewhat more dilated (Fig. 14B). 16–26 mm. Western Cape mountains . . . . . *C. cameroni* Barnard



- 7 (6) Ventral process of mandible indistinct, situated in a basal position not surpassing mentum. Dorsal process about median in position, narrow, cylindrical, perpendicular to main arm (Fig. 11C). Anterior tibia distinctly arcuate at apical portion (Fig. 14E), ventral crest evenly and sharply elevated from base, abruptly contracted postmedially, forming a right angle (Fig. 14F). Apico-ventral process entirely in inner marginal position, also visible in dorsal view (Fig. 14E). 17–22,5 mm. Western Cape mountains. . . . . *C. eastmani* Barnard
- 8 (1) Anterior margin of clypeus sharply elevated above the level of labrum. Aedeagus of asymmetrical type, left and right parameres strongly dissimilar, the left one angularly dilated (Fig. 5B). Penis strongly sclerotized, surface smooth with longitudinal lateral margination, apex asymmetrical (Fig. 5C).
- 9 (10) Mandibles long, beak-like and prognathous with matching inner margin (Fig. 21B), together with legs orange-brown in contrast to black body; small ventral processes in basal position. Anterior tibia straight, evenly dilated with four sharp lateral teeth (Fig. 20A). 28–35 mm. Swartberg range. . . . . *C. primosi* Barnard
- 10 (9) Mandibles arcuate, black.
- 11 (12) Anterior tibia narrow, rectangularly bent inward in apical third (Fig. 27F). Ventral process of mandibles in apical position; apex of main arm in closed position of mandibles forms a circle with ventral process (Fig. 29C). Pronotum about as long as broad, normally with a pair of red dots on disc (Fig. 31). 21,8–25,3 mm. Langeberg range. . . . .  
. . . . . *C. izardi* Barnard
- 12 (11) Anterior tibia straight or bent at varying angles, but not rectangularly bent or filiform.
- 13 (14) Anterior tibia flat and oblong with parallel margins, about three times longer than broad (Fig. 27A); ventral crest sharp at basal half of length, ending here abruptly, forming a rectangle. Apico-ventral process large. Mandible with ventral process only (Fig. 21A). 15–19 mm. Swartberg range. . . . . *C. neli* Barnard
- 14 (13) Tibia not regularly oblong.
- 15 (16) Frons behind clypeal declivity with a rounded elevation. Main arm of mandibles broadly truncate and slightly bifid at apex, with rounded dorso-median elevation. Dorsal process reduced to a tiny basal knob. Basally situated ventral process small, hardly surpassing labrum (Fig. 24A). Anterior tibia moderately arcuate and dilated with four or five often irregular lateral processes (Fig. 20B). 21–25 mm. Table Mountain. . . . . *C. westwoodi* Gray
- 16 (15) Frons flat in middle or finely concave at clypeal declivity.
- 17 (20) Mandible without dorsal process.

- 18 (19) Anterior tibia very strongly dilated from base to apical four-fifths, then abruptly reduced into a U-shaped emargination before rising into bifid apico-lateral process (Fig. 27B). Pronotum deeply emarginate posteriorly, posterior angle rectangular. 23–27,8 mm. Swartberg range. . . . .  
 . . . . . *C. montisatris* sp. nov.
- 19 (18) Basal three-fifths of anterior tibia almost straight and parallel in dorsal view, apical dilation trifid, not contracted before dilation (Fig. 20E). Posterior third of pronotum contracted, but lateral margin here not concave, posterior angle of pronotum obtuse-angled, ampliate lateral margin of disc rounded. 21 mm. Langeberg range. *C. barnardi* sp. nov.
- 20 (17) Mandibles with dorsal and ventral processes.
- 21 (22) Anterior tibia very strongly dilated from base to deep pre-apical emargination of lateral margin; apico-lateral process narrow and bifid (Fig. 27D). Dorsal process of mandibles in median position forming an oblong surface with pointed angle at its inner apical corner; the whole process is sunk below the dorsal level of the main arm. Ventral process with its forward-pointing apex is positioned between the apex of main arm and dorsal process (Fig. 29A). 26–31 mm. Swartberg range. . . . .  
 . . . . . *C. whitei* Barnard
- 22 (21) Anterior tibia not strongly dilated laterally, tibia semi-parallel, expanding evenly to apical process. Dorsal process of mandibles is not an oblong structure.
- 23 (24) Ventral process of mandibles is produced sharply forward; it is narrow and cylindrical. According to the shape and position of the dorsal processes this species is known in two sympatric morphs (Fig. 17B, C). More than 18 mm. Western Cape mountains. . . . . *C. cassoni* Barnard
- 24 (23) Ventral process of mandibles forms a forward-upward slanting ridge from base, its corners are rounded obtuse-angled (Fig. 19). Dorsal process pointed triangular. Length about 21 mm. Swartberg range. . . . .  
 . . . . . *C. berrisfordi* Barnard

## DESCRIPTIONS OF THE SPECIES

## THE PLESIOMORPH GROUP OF SPECIES

The common characters of the species forming this group are the symmetrical type of aedeagus (Fig. 5A) and evenly arcuate posterior margin of anal sternite in males. A correlated character is the structure of the forehead, where the margin of the clypeus is level with the labrum (in males). Phenetic characters do not show the split into the two main lineages in females.

The parameres in this species group are nearly similar, symmetrically arcuate at their apex, with the left paramere also simple (enlarged in the species of the apomorphic group). Penis less sclerotized than in the apomorphic species, with characteristic undulation on the shaft. Apex evenly and symmetrically rounded, ending in the long flagellum of the ductus ejaculatorius. Minor differences were

seen between species in minute details of the aedeagus; however, these will not be described, as no particular importance was attributed to them in the evaluation. External characters of males were found to be sufficiently constant and much more evident than those of the aedeagi. In *C. stokoei*, the only species where considerable variability of characters could not be evaluated conclusively (individual or subspecific), there are not enough males known to provide the support of genital characters.

*Colophon cameroni* Barnard, 1929

Figs 11A, 12, 14B

*Colophon cameroni* Barnard, 1929: 172, fig. 7; 1932a: 23, figs. Didier & Séguy, 1953: 76. Brinck, 1956: 309, 320. Holloway, 1960: 335.

*Diagnosis*

Black, medium size; mandible with large dorsal and small ventral processes. Anterior tibia almost straight, ventral crest sharply elevated basally, flat apically with apico-ventral process. Aedeagus of symmetrical type.



Fig. 11. Male mandibular structure in *Colophon* species. A. *C. cameroni* Barnard. B. *C. haughtoni* Barnard. C. *C. eastmani* Barnard.

*Description*

*Male.* Head broad and short, slightly tapering in front of eyes; rounded ocular canthi high, vertex flatly depressed between. Frons steeply deflected towards clypeus, which is level with flat and broad labrum. Punctuation finer and denser near ocular canthi than at vertex. Mandibles prognathous, finely and evenly arcuate, pointed apex not bent inward. Dorsal process large, slightly raised above the level of main arm; slightly forward-pointing, truncate apex slightly dilated. Ventral process short and broad at base of mandible, rounded apex rectangular or obtuse-angled (Fig. 11A). Mentum more than twice as broad as long, corners narrowly rounded, anterior margin arcuately truncate. Gular sulcus shallow.



Pronotum distinctly broader than elytra, lateral margins semi-parallel (hardly converging forward) in median third, more convergent in anterior third, posteriorly not emarginate. Lateral and basal margins margined, anterior margin smooth. Punctuation very fine and scattered.

Elytra smooth, densely shagreened and very finely punctate, wanting distinct subhumeral carina.

Anal sternite only slightly asymmetrical.

Anterior tibia straight, evenly dilated from base to apex; bifid apico-lateral process short and broad, not marked off basally by deep insinuation of lateral margin (Fig. 14B). Ventral crest sharply elevated in basal two-thirds, gradually flattened anteriorly; apico-ventral process small.

Aedeagus of symmetrical type. Penis feebly sclerotized, apex symmetrical and smoothly rounded, shaft sharply and deeply wrinkled transversely. Parameres



Fig. 12. *Colophon cameroni* Barnard, male; paralectotype; length 24,5 mm.

relatively symmetrical, right paramere broader, apex more pointedly turned inward; left paramere narrower, inward-turning apex short and rectangular.

*Female.* No female is known from the type locality.

#### *Length*

Male: 25 mm (range, estimated from heads, 16–26 mm).

#### *Distribution*

Western Cape, Hex River Mountains.

#### *Material examined*

Males: 3 complete specimens, 1 anterior part of body, 24 heads and 10 anterior legs. Females: 3 complete specimens, 2 bodies and 1 head. Lectotype ♂, paralectotype ♀ (complete); 1 ♂ and 1 ♀ (complete), 4 ♂ heads (paralectotypes) in British Museum (Natural History), London. All other specimens in South African Museum, Cape Town.

*Lectotype.* ♂: Waai Hoek Mts., 5 000 ft. [= 1 524 m], 1.1.1925, K. H. Barnard, in British Museum, London.

*Paralectotypes.* 1 complete ♂, 7 ♂ heads and 5 ♂ anterior legs: Waai Hoek Mts., 5 600 ft. [= 1 707 m], [April] 1928, K. H. Barnard in South African Museum, Cape Town; 1 complete ♀, Waai Hoek Mts., 5 600 ft. [= 1 707 m], in British Museum, London. 17 ♂ heads (13 in South African Museum, 4 in British Museum): Fonteintjieberg, Worcester distr., 6 500 ft. [= 1 982 m], [March] 1929, K. H. Barnard.

*Additional material.* 1 ♂, 1 ♀, Milner Ridge Peak, Hex River Mountains, 6 000 ft. [= 1 829 m], January 1934, K. H. Barnard, in British Museum, London. 1 ♂, 2 ♀ (specimens found dead) and 2 ♂ anterior legs: Great Winterhoek top, 6 800 ft. [= 2 073 m], August 1929, K. H. Barnard, in South African Museum. 3 ♂ anterior legs: Witzenberg range, Tulbagh, 1932, F. Berrisford, in South African Museum.

#### *Variability*

There is a considerable size variation in the 21 ♂ heads measured. They range between 4 and 6 mm, measured between transverse sulcus of vertex and apex of mandibles. No allometric variation was found. A limited individual variation could be observed in the angle of the basal process of mandibles, and in the apical curvature of mandibles, as well as in the length of the ventral elevation of anterior tibia. Nevertheless, the Waai Hoek and Fonteintjesberg specimens are certainly conspecific.

A pair from Milner Ridge Peak, Hex River Mountains (see above) represent the smallest specimens [♂ 16 mm, ♀ 17 mm]. Head length of male (measured as above) is only 3,7 mm. In this male the mandibular structure is similar but the dorsal processes are narrower and are not dilated at their apex; ventral process flat, obtuse-angled. Elytra in both specimens with faint and short subhumeral

elevation. Anterior tibia similar, but elevation of ventral crest less than half of tibial length.

*Colophon haughtoni* Barnard, 1929

Figs 11B, 13, 14D

*Colophon haughtoni* Barnard, 1929: 171, fig. 6; 1932a: 19, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 308, 320.

*Diagnosis*

Black; pronotum and elytra more shiny than in the other species. Medium size. Pronotum immarginate anteriorly. Anal sternite moderately asymmetrical, aedeagus of symmetrical type.

*Description*

*Male.* Head broadly oblong. Genal margin in front of eye distinctly emarginate. Ocular canthus high but rounded, vertex evenly concave in between, steeply deflected in middle to broad and finely emarginate clypeus, which is on the same level as the labrum. Punctuation of vertex distinct, somewhat denser laterally. Mentum broad, semicircular. Transverse gular sulcus broad and rather shallow. Mandibles moderately long, evenly arcuate from base to apex. Apex appears as split, inner dorsal portion being curved backwards to form a broad concave surface between the two apices. Dorsal process absent. Ventral process small and obtuse-angled at base of mandibles (Fig. 11B).

Pronotum broadest at about the basal third of its length, evenly arcuate anteriorly in one, roundly arcuate to apical angle in another specimen. Prebasal section of lateral margins contracted but not emarginate. Posterior angle obtuse. Anterior margin of pronotum immarginate. Disc very finely and sparsely punctate, punctures somewhat larger laterally. Base of prosternal apophysis without a trace of callous elevation.

Elytra short and broad, not much narrower than pronotum. A short humeral crest at base distinct and, particularly in one of the two males, a faint longitudinal striation discernible.

Anal sternite moderately asymmetrical.

Anterior tibia arcuate, moderately dilated towards apex with an apical and a pre-apical triangular process, which appears in some other species as the bifid apico-lateral process (Fig. 14D). Ventral crest sharp and elevated in basal two-thirds, flattened pre-apically, forming a very large conical process perpendicular to tibia.

Aedeagus of symmetrical type. Penis feebly sclerotized together with apical portion. Parameres (right) unarmed pre-apically, apical portion of parameres nearly symmetrical.

*Female.* Shape of pronotum and elytra, and sculptural features of latter, similar to that of males.



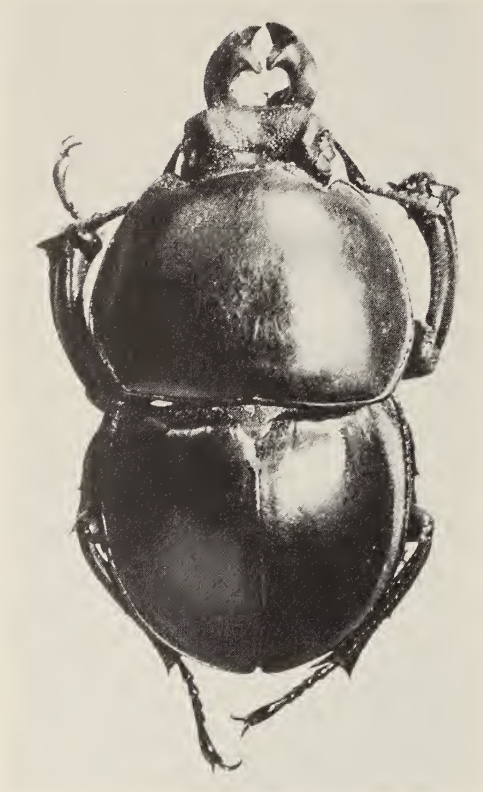


Fig. 13. *Colophon haughtoni* Barnard, male; length 23 mm.

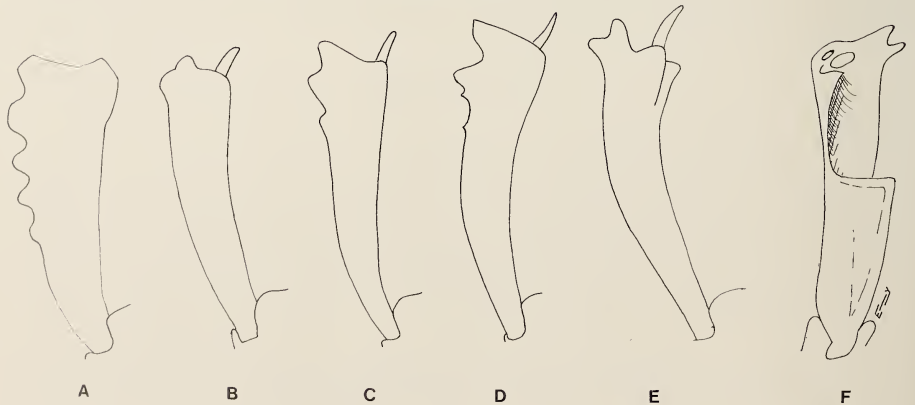


Fig. 14. Anterior tibiae in *Colophon* species. A. *C. primosi* Barnard, female. B. *C. cameroni* Barnard, male. C. *C. cassoni* Barnard, male. D. *C. haughtoni* Barnard, male. E. *C. eastmani* Barnard, male. F. *C. eastmani* Barnard, male in semi-ventral view.

*Length*

Males 20–23 mm, female 18 mm.

*Distribution*

Hex River Mountains.

*Material examined*

*Holotype*. ♂: Matroosberg, Hex River Mountains; 1917, S. H. Haughton; in British Museum (Natural History), London.

*Additional material*. 2 ♂, 1 ♀: Matroosberg, Hex River Mountains; January 1941, K. H. Barnard, in South African Museum, Cape Town. 2 ♀ (found dead): Groot Hoek Peak, Hex River Mountains; September 1933; K. H. Barnard, in British Museum, London.

*Colophon eastmani* Barnard, 1932

Figs 11C, 14E–F, 15

*Colophon eastmani* Barnard, 1932b: 174, fig. 6. Didier & Séguy, 1953: 76. Brinck, 1956: 309, 320.

*Diagnosis*

Medium-sized black species. Mandible with dorsal process in middle and ventral process basally. Clypeus is flush with labrum, pronotum immarginate anteriorly. Anterior tibia in male moderately arcuate with bifid apico-lateral process. Anal sternite moderately asymmetrical, aedeagus of symmetrical type.

*Description*

*Male*. Head transversely oblong. Genal margins in front of eye emarginate, not converging. Ocular canthi large, broad and rounded, vertex evenly concave in between, anteriorly straight or shallowly sinuate. Vertex steeply deflected to clypeus. Clypeus broadly truncate or finely emarginate; flush with broad and flat triangular labrum. Disc finely and rather sparsely punctate. Mandible evenly arcuate, sickle-shaped apex pointed, perpendicular dorsal process behind middle with large rounded apex. Ventral process very short, pointed, obtuse-angled; in closed position of mandibles concealed by labrum (Fig. 11C). Mentum flat, twice as broad as long, laterally evenly arcuate. Transverse gular sulcus deep, anteriorly vertical.

Pronotum moderately broader than elytra, broadest between middle and posterior third of length; lateral margins almost evenly arcuate between lateral angles, posteriorly flattened but not emarginate, posterior angle rounded obtuse-angled. Pronotum anteriorly immarginate. Punctuation hardly visible on disc, more distinct laterally.

Anal sternite forms a small callus at margin, which is almost in middle; hardly asymmetrical.



Fig. 15. *Colophon eastmani* Barnard, male; paralectotype; length 22 mm.

Anterior tibia moderately arcuate inward, slightly dilated, apico-lateral process produced, bifid (Fig. 14E, F). Ventral crest sharp, gradually elevating to abrupt end in front of middle; apico-ventral process small, triangular, forward-pointing, visible in dorsal view (Fig. 14E, F).

Aedeagus of symmetrical type. Penis feebly sclerotized. Parameres not quite symmetrical.

*Female.* Unknown.

*Length*

Male 17–22,5 mm (lectotype 22,5 mm).

*Distribution*

Western Cape mountains.

*Material examined*

6 ♂ (dead), 2 ♂ heads, 10 ♂ anterior legs.

*Lectotype.* ♂: Keeromberg (Worcester), Sept. 1930; K. H. Barnard, in British Museum, London.



*Paralectotypes*. 1 ♂: Keeromberg (Worcester), Sept. 1930; K. H. Barnard, in British Museum, London. 3 ♂ (partially fragmented), 2 ♂ heads, 10 ♂ anterior legs; Keeromberg (Worcester), Sept. 1930; K. H. Barnard, in South African Museum, Cape Town.

*Additional material*. 1 ♂ (fragmented): Dassieberg, Robertson, 5 550 ft. [= 1 692 m]; January 1936, K. H. Barnard; South African Museum.

*Colophon stokoei* Barnard, 1929

Figs 16, 17A, 20C–D

*Colophon stokoei* Barnard, 1929: 168, figs 3–5. Didier & Séguy, 1953: 77. Brinck, 1956: 308, 320.

*Diagnosis*

A species with symmetrical type of aedeagus and anal sternite; clypeus flush with labrum. Mandibles without dorsal process, anterior tibiae arcuate, apically bifid in front of lateral emargination. Mentum prominently thickened.

*Remarks*

A range of variations was described as 'local variation' by Barnard, who marked the different types as 'f. typ. [forma typica], var. A, B, C, and D'. Considering the large and fragmented distribution area of *C. stokoei*, the marked differences could indicate subspecifically distinct populations. The locality records, however, seem to contradict such a situation. One of Barnard's reasons for not attaching specific or subspecific value to any of these variations could have been the inconclusive distribution patterns drawn from the available records. Some of the locality data, often provided by laymen, are considered as doubtful (e.g. the Blesberg record of *C. whitei*, see p. 417), and no further records have become known since Barnard's (1929) description. Though I doubt that some of the considerable differences are due only to individual variations, I refrain from drawing any conclusions due to the inadequacy of the material. The differences will be briefly discussed and the varieties are denoted below by the same letters as used by Barnard.

*Description*

*Male*. Head transversely oblong, anterior lateral angle almost pointed, but more obtuse-angled than in *C. westwoodi*. Internal subocular crests rounded but distinct, with tubercle at the anterior inner end of each crest. Frons evenly depressed between tubercles and arcuately slanting to clypeus. Barnard's 'anterior margin of head' refers to the angle of declivity of frons towards clypeus and not to a difference in levels between clypeus and labrum. The shape of frons and its form of declivity show a high degree of variation. It is sharp-edged with an overhanging clypeus in *C. stokoei* var. B. Clypeus meets triangular labrum on the same level.

Mandibles comparatively short and simple, each nearly semicircular, dorsal surface of apical portion furcate. Dorsal process lacking. Ventral process

prominent, rectangular (*C. stokoei* var. C) or forward-pointing acute-angled (Fig. 17A).

Mentum very thick with a high degree of variation (simple in all other species). The actual form of mentum is the basis of Barnard's division of the species into varieties. In all varieties mentum evenly elevating from base in lateral view, and forming a vertical line or surface anteriorly. Anterior margin transverse, sometimes more or less tuberculate at either side (*C. stokoei* forma typica and *C. stokoei* var. B), anterior surface broad and large, deeply excavated (*C. stokoei* var. A), or simply roundly pointed (*C. stokoei* var. C and D).

Pronotum evenly arcuate at lateral margins, hardly and only very slightly emarginate near posterior angle. In general appearance moderately enlarged.

Elytra short and broad with distinct variation in proportions. Smooth in most varieties but in the 'holotype' of *C. stokoei* var. C, elytron with two distinct lateral elevations and a rounded inner longitudinal elevation (costae).

Anterior tibia more or less arcuate and dilated towards apex. Apex laterally bifid (*C. stokoei* forma typica, var. A, B and D) with deep U-shaped emargination pre-apically (Fig. 20C) (*C. stokoei* forma typica, var. A and B, less deep in *C. stokoei* var. D); or apico-lateral armature tridentate with indistinct pre-apical emargination (*C. stokoei* var. C) (Fig. 20D). Ventral longitudinal crest distinct, but not sharply raised basally, almost continuous to apex in *C. stokoei* var. C. Apico-ventral process long and narrow in all varieties.

Aedeagus of symmetrical type and similar in all varieties where known (*C. stokoei* forma typica, var. A and C) and all seven dissected specimens. As specific differences in aedeagi can be found between all recognized species of the genus, the similarity of aedeagi in *C. stokei* varieties might indicate their infraspecific status. Dorsal line of left paramere in lateral view emarginate in apical third, and forms an angle where it turns into the finely convex basal two-thirds; in *C. haughtoni* apical portion almost straight, angle flat and indistinct. Right paramere less pointed than in *C. haughtoni*.

*Female.* Apparently identical between varieties where known (i.e. from localities of *C. stokoei* forma typica, var. B, C and D).

#### *Length*

Male 24–27 mm, female 18–22 mm (Barnard (1929)—20–22 mm in males, measured without mandibles).

#### *Distribution*

Western Cape mountains from Hottentots Holland to the Stellenbosch and Wellington mountains.

#### *Material examined*

10 ♂ (two dismembered and seven dissected), 4 ♀. Of these 2 ♂ and 2 ♀ are in British Museum (Natural History), London; all other specimens in South African Museum, Cape Town.

*Type material.* The designation of a primary type should actually only be applied to the 'forma typica' described by Barnard as *C. stokoei*; specimens listed under his lettered varieties should not be designated as paralectotypes of the same species. However, I intend to designate primary types for the 'varieties' as well, so as to avoid increasing the existing confusion, not only in the evaluation of the variability of the species but probably also in the given locality records. The label data are quoted exactly from the specimen labels and additional information, partly from Barnard (1929), is given in brackets.

*C. stokoei* forma typica

*Lectotype.* 1 ♂: Hott.-Holl. [Hottentots Holland] Mts., 4 000 ft. [4 000–5 000] ft. [= 1 220–1 524 m], Caledon C.C. [Cape Colony], Barnard, [January] 1916; in British Museum, London.



Fig. 16. *Colophon stokoei* Barnard, male; paralectotype of Barnard's forma typica; length 24 mm.



*Paralectotype*. 1 ♂: data as for lectotype; in South African Museum, Cape Town.

A third male with identical data to the above specimens, but not mentioned in Barnard's (1929) description, is in the South African Museum, Cape Town. It is identical to the 'lectotype' of *C. stokoei* var. A (see below).

*C. stokoei* var. A.

'Lectotype', ♂: Kleinmond Mt., C.P. [Cape Province]; 1.8.1927, T. P. Stokoe, in the South African Museum, Cape Town.

The identity of this specimen, the second listed by Barnard (1929), is not quite certain, though the area, date and collector agree. The first specimen listed by Barnard as *C. stokoei* var. A could not be found, unless it is the one listed above but bearing different locality. Though both specimens agree with the description of *C. stokoei* var. A, they prove how unreliable the locality data are.

*C. stokoei* var. B.

Syntypes consisting of 1 ♂ head, 1 ♀ head, 4 ♂ anterior legs (rather dissimilar in details): Plattberg, 3 000 ft. [915 m], Palmiet Riv. Mts., K. H. Barnard, Febr. 1927 [South African Museum]. Syntype, 1 ♀ (dismembered): locality as for other syntypes; in British Museum (Natural History), London.

*C. stokoei* var. C.

Holotype, ♂: Drakenstein Peak [Stellenbosch District], 4 000 ft. [1 220 m], 2.1.1920; K. H. Barnard [and T. P. Stokoe]; in South African Museum, Cape Town.

*C. stokoei* var. D.

Syntypes consisting of 1 ♂ head and 3 ♂ anterior tibiae: Up. [Upper] Snoukop, Wellington 4 500 [-5 000] ft. [= 1 372-1 524 m], K. H. Barnard [and R. Primos], [January].

*Additional specimens*. 1 ♂ (forma typica): Sneekop, Hottentots-Holland Mts., Somerset West (name of collector illegible), 20.xii.1945. 1 ♂ (forma typica): Bushmans Castle, Berg River Range, Franshoek, Dec. 1943. 1 ♂ (closest to *C. stokoei* var. C, but more slender and straight anterior tibia): Sneekop, Hottentot-Holland\* Mts., 4 500 ft. [1 372 m], 15.xii.1935, K. H. Barnard. 2 ♂ and 2 ♀ (morphologically between *C. stokoei* forma typica and *C. stokoei* var. C): Berg River Range, Emerald Dome, Apr. 1944, K. H. Barnard. 1 ♀ (see Barnard 1929, *C. stokoei* var. C): Helderberg, 5.xii.1926, K. H. Barnard.

THE APOMORPH GROUP OF SPECIES

The common characters of this species group are the strongly asymmetrical shape of the aedeagus and the correspondingly asymmetrical posterior margin of the anal sternite in males. A correlated character expressed in the same form in all the species of this group is the anterior margin of the clypeus being raised above the level of the labrum. As the asymmetry of the aedeagus and the position of the labrum are not functionally related, these correlated apomorphic characters indicate convincingly the monophyletic origin of this well-defined evolutionary lineage.

The parameres in these species are asymmetrically expanded, with the left-hand one in particular forming a large apical or pre-apical triangular process pointing towards the penis. Thus the two parameres form a closed sheath or funnel around the penis in a closed position, probably in order to protect the penis and the long flagellum at penetration at the start of copulation. (Note that the flagellum is not retractile into the penis as it is in the Lampriminae.) The penis is strongly sclerotized, its apical portion asymmetrical. Its integument is firmly sclerotized with longitudinal furrows (Fig. 5B) and is not transversely undulating as in the plesiomorphic species group (Fig. 5A). The posterior margin of the anal sternite is emarginated above the enlarged left paramere and bears a more-or-less (according to species) distinct, rounded projection above the right paramere (Fig. 5D). More or less distinct differences in the structure of the parameres and the penis were observed between species. Although these differences are likely to be constant and specific, a detailed evaluation was not possible owing to the scarcity of the material. While male genital characters might improve the phylogenetic evaluation of the species, their importance in species identification is limited, as male external characters are ample and appear to be specifically constant.

*Colophon cassoni* Barnard, 1932

Figs 14C, 17B–C, 18

*Colophon cassoni* Barnard, 1932b: 172, fig. 4. Didier & Séguy, 1953: 76. Brinck, 1956: 311, 320.

*Diagnosis*

Small to medium-sized black species. Male mandibles with dorsal and prominent ventral processes. Aedeagus of asymmetrical type.

*Description*

*Male.* Head broadly oblong. Genal margin in front of eye straight, parallel or slightly converging. Anterior margin deeply insinuated and deflected to vertically positioned clypeus. Clypeus narrow, pointed in small specimens, raised above

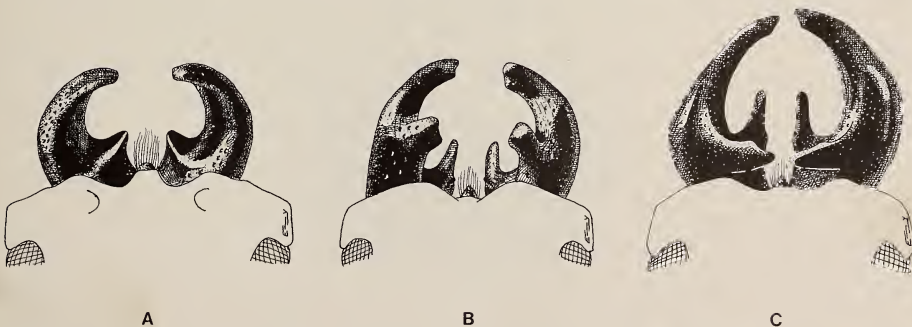


Fig. 17. Male mandibular structure in *Colophon* species. A. *C. stokoei* Barnard (forma typica). B. *C. cassoni* Barnard (forma typica). C. *C. cassoni* m. *recurva* morpha nov.

level of small triangular labrum. Mandibles rather short, main arms curved inwards at varying angles. Apices roundly pointed or truncate, sometimes slightly emarginate. Ventral process sharply produced anteriorly, joining the main arm, slightly sinuate at its inner margin; apex reaches basal third to half of length of mandible. Dorsal process thick, almost cylindrical, rising smoothly from surface of main arm, pointing slightly forward (Fig. 17B). Mandibular armature is subject to allometric variation. Mentum slightly convex, roundly triangular, coarsely punctate. Gular sulcus flat.

Pronotum hardly broader than elytra in specimens seen (all small). Margins semi-parallel in median third, evenly arcuate, converging anteriorly, finely emarginate behind. Pronotum with margination only interrupted in middle of anterior margin. Punctation extremely fine on disc, more distinct at posterior angle.

Elytra smooth, finely punctate, sutural margins smoothly and rather indistinctly elevated.

Anal sternite asymmetrical, without distinct off-centre protuberance of margin (small specimen).

Anterior tibia similar to that of *C. cameroni*; almost straight at inner margin, arcuately dilated towards apex. Bifid apico-lateral process more produced, sometimes with a third rudimentary proximal process (Fig. 14C). Ventral crest sharply elevated at basal two-thirds (some variation in length), arcuately interrupted pre-apically; apico-ventral process rather large; in an inner-side view the process looks as if split from body of tibia.

Aedeagus: right paramere forms a large process at its inner margin; margin between process and apex straight, angularly emarginate between process and base. Left paramere unarmed, wedge-shaped with roundly pointed apex.



Fig. 18. *Colophon cassoni* Barnard, male; paralectotype, fragment; length 14 mm. An estimated total length of the specimen could be about 23 mm.



*Female.* Distinguished by the anterior margination (interrupted in middle) of pronotum, emargination of posterior converging portions of pronotal margins, smooth and rather broad fine elevation of sutural margins. Pronotal punctation more distinct than in male.

#### *Length*

Male 18 mm (range estimated from size of heads 16–24 mm); female 16–17 mm.

#### *Distribution*

Swartberg, the northern range of Cape mountains.

#### *Variability*

The mandibular armature of males shows two distinct forms, without any intermediates. Barnard (1932*b*: 172) referred to intermediates but these differed only in thickness and shape of the apex of the dorsal processes (as is often seen in the genus) and not in the position and direction of the processes. No similar dimorphism has been seen in any other species of the genus. However, as no correlated characters could be found and only one complete male is known of each form, the actual value of this unusual difference cannot be evaluated. All specimens and fragments referred to this species were collected on two occasions (1930 and 1932) and both samples include both mandibular forms. It can thus be assumed that the two forms occur sympatrically. For the time being the two varieties will be considered as morphs of the same species (see below).

*Colophon cassoni* Barnard, 1932 (forma typica)

Fig. 17B

#### *Description*

Dorsal process of mandibles in median position, pointing diagonally forward. With mandibles in closed position, the small space bounded laterally by the main arms and apically by the dorsal processes is of an inverted heart-shape (Fig. 17B).

#### *Material examined*

*Lectotype.* ♂: Meiringspoort Berg, Zwartberg Range, K. H. Barnard, Febr. 1932; in British Museum (Natural History), London.

*Paralectotypes.* 1 ♀ (identity doubtful); Meiringspoort Berg, Zwartberg range, K. H. Barnard, Febr. 1932; in British Museum, London. 21 ♂ heads, 26 ♂ anterior legs; data as for lectotype; in South African Museum, Cape Town. 2 ♀ (identity doubtful), 3 ♂ heads, Meiringspoort Berg, Zwartberg Range, F. Berrisford, 1930; in South African Museum.

*Colophon cassoni* *morpha recurva* morph. nov.

Fig. 17C

*Description*

Dorsal process of mandibles in basal position pointing diagonally backward. Space between the apex of mandibles and dorsal processes ovate and much larger (Fig. 17C).

*Material examined*

*Holotype*. ♂: Meiringspoort Berg, Zwartberg Range, Febr. 1932, K. H. Barnard; in British Museum (natural History), London.

*Paratypes*. 2 ♂ heads (data as for holotype); 1 ♂ front body, 2 ♂ heads (data as for holotype, but coll. F. Berrisford, 1930); in South African Museum, Cape Town. ♂ head (data as for holotype) in Transvaal Museum, Pretoria.

*Remarks*

Barnard's (1932*b*) description gave the data for specimens collected by F. Berrisford as 'Blaauw Punt near Meiring's Poort, Zwartberg Range, 6 500 ft. (F. Berrisford and P. Casson Scott-Hayward), March 1930'. As is often the case, the data published by Barnard are not consistent with those of the labels; there is no doubt, however, that they refer to the same specimens.

The identity of Meiringspoort Berg could not be established among the peaks west of the poort.

*Colophon berrisfordi* Barnard, 1932

Fig. 19

*Colophon berrisfordi* Barnard, 1932*b*: 173, fig. 5; 1932*a*: 19, figs. Didier & Séguy, 1953: 76. Brinck, 1956: 311, 320.

*Remarks*

The holotype (the only specimen known) is a fragment, generally in a fresh condition, consisting of the front part of the body of a male (head with both antennae and pronotum with both anterior legs, one complete with tarsi). The aedeagus and anal sternite, which bear the most important species-group characters, are wanting. Sharp-edged clypeus, elevated above labrum, refers the species to the apomorphic group, as this character is correlated with the asymmetrical type of aedeagus in all known species. Structure of anterior tibia is practically identical with that of *C. cassoni*, and rather similar to that of *C. cameroni*.

*Description*

*Male*. Head very similar to that of *C. whitei*, with the sharp and narrow transverse dorsal impression level with eyes; genal canthus in front of eye less dilated. Moderately arcuate mandibles with well-developed premedian dorsal

process, and with small tubercle between this process and apex (more distinct on left mandible). Ventro-basal process of mandible forms a forward- and upward-slanting ridge with rounded corners (Fig. 19).

Pronotum sharply margined all round, marginal fossa only flattened at a point in middle of anterior margin. Shape similar to *C. whitei*, surface densely shagreened, punctation extremely fine in middle of disc, gradually more distinct towards lateral margins.

Anterior tibia slightly arcuate, semi-parallel to apical dilation, not contracted pre-apically. Apical dilation armed with three teeth. Ventral crest strongly elevated from base to in front of middle, here almost forming a right angle, arcuately flattened to the base of the small rectangular apico-ventral process. Ventral crest and apico-ventral process are comparable to those of *C. neli* and *C. cassoni*. Inner apical corner of tibia forms a sharp, slightly acute-angled process, not rounded as in *C. neli*.

*Female.* Unknown.

#### *Length*

From apex of mandibles to base of pronotum 13 mm, breadth of pronotum 10,0 mm, suggesting a smaller specimen than the smallest known specimen of *C. whitei*; total length probably in the range of 20–22 mm.

#### *Distribution*

Central part of Swartberg Range, west side of Meirings Poort.



Fig. 19. *Colophon berrisfordi* Barnard, male; holotype, fragment; length 13 mm. An estimated total length of the specimen could be about 21 mm.



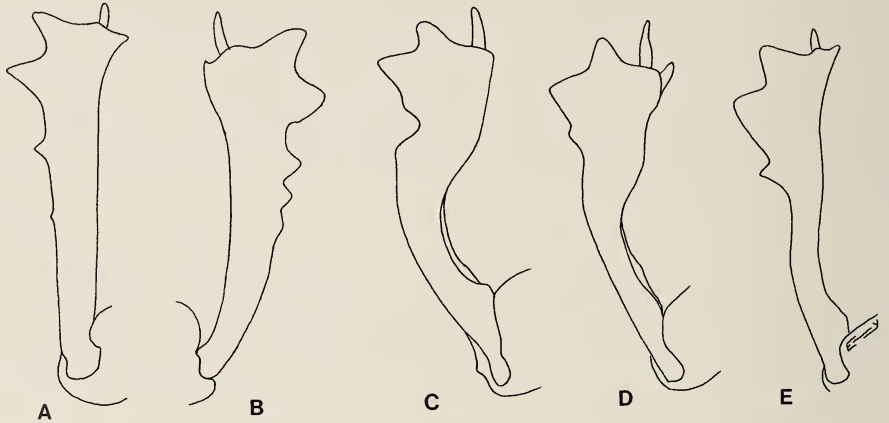


Fig. 20. Male anterior tibiae in *Colophon* species. A. *C. primosi* Barnard. B. *C. westwoodi* Gray. C. *C. stokoei* Barnard forma typica from Bushmans' Castle. D. *C. stokoei* Barnard, holotype of Barnard's var. C. E. *C. barnardi* sp. nov.

#### Material examined

*Holotype*. ♂ (anterior part of specimen): Meirings Poort Berg, Zwartberg range, F. Berrisford, 1930; in British Museum (Natural History), London. (Name label in Barnard's hand.)

#### *Colophon neli* Barnard, 1932

Figs 21A, 27A

*Colophon neli* Barnard, 1932b: 170, fig. 2; 1932a: 19, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 310, 320.

#### Diagnosis

*Colophon neli* is the smallest known species of the genus. Black. Mandible lacking dorsal process. Anterior tibia broad, straight and parallel. Clypeus raised above labrum. Anal sternite and aedeagus of asymmetrical type.

#### Description

*Male*. Head broadly oblong. Ocular canthus and a pair of anterior elevations at the base of the mandibles rounded. Vertex deflected in a V-shape to clypeus, which is narrow with rounded or emarginate apex and is raised high above narrow triangular labrum. Surface coarsely punctate, particularly in depressions. Mandible simple sickle-shaped, with only prominently pointed ventral process at the base (Fig. 21A). Gular sulcus very flat and shallow.

Pronotum broadest at about basal third of length; lateral margins evenly arcuate, converging anteriorly, finely emarginate towards obtuse-angled posterior angle. Margination only interrupted in middle of anterior margin. A fine punctation of surface visible only near the posterior angle. Base of prosternal apophysis not calloused as in most species.

Elytra conspicuously small in relation to large pronotum, almost circular. Broad sutural margins smooth and raised. No subhumeral callus or other conspicuous longitudinal sculptural elements. The very fine shagreen produces an iridescent sheen on the elytra of fresh specimens (lectotype).

Anal sternite asymmetrical, but does not form an off-centre callus.

Anterior tibia broad from the base, straight and parallel, it forms a short and broad bifid apico-lateral process (Fig. 27A). Ventral crest sharp and well raised basally, then terminates abruptly between half and two-thirds of tibial length, forming a rectangle; after a short stretch of interruption forms a small triangular process near apex.

Aedeagus asymmetrical. Penis strongly sclerotized, apical portion asymmetrically dilated. Right paramere forms a broad triangular process at its inner margin, well removed from apex of paramere; margin between apex and inner process slightly emarginate. Left paramere contracts towards apex, apex rounded.

*Female.* It resembles *C. cassoni* in raised suture line, which is less distinct than in male. Anterior tibia, however, has an apico-ventral process, which is absent in *C. cassoni*.

#### *Length*

Male 15–19 mm, female 15–17 mm.

#### *Distribution*

Swartberg Mountains, the northern range of the Cape mountains.

#### *Material examined*

7 ♂, 3 ♀, 1 ♂ front body, 14 ♂ heads, 3 ♀ heads, 12 ♂ anterior legs.

*Lectotype.* ♂: Swartberg Pass, K. H. Barnard, Nov. 1929; in South African Museum, Cape Town.

*Paralectotypes.* 3 ♂, 2 ♀, 8 ♂ heads, 9 ♂ anterior legs: Swartberg Pass, K. H. Barnard, Nov. 1929; in South African Museum, Cape Town. 3 ♂, 1 ♀: Swartberg Pass, K. H. Barnard, Nov. 1929; in British Museum (Natural History), London.

*Additional material.* 1 ♂ front body, 6 ♂ and 3 ♀ heads, 3 ♂ anterior legs: Swartberg Pass, Dec. 1968, R. H. Jones and J. H. Potgieter; Transvaal Museum, Pretoria.

#### *Remarks*

The altitude data on the labels of some of the type specimens range between 5 500 and 6 000 ft. [1 677 m and 1 829 m], and not 5 500 and 6 500 ft. [1 677 m and 1 982 m] as stated in Barnard's (1932*b*) description.

*Colophon primosi* Barnard, 1929

Figs 14A, 20A, 21B, 22A-C

*Colophon primosi* Barnard, 1929: 175, fig. 9; 1932a: 19, figs. Didier & Séguy, 1953: 76. Brinck, 1956: 314, 320.

*Description*

*Male*. Head broadly oblong, rather similar to that of *C. izardi*, but ocular corner not sharply raised. Vertex only depressed, frons level transversely and only slightly deflected to produced clypeus, which is very highly elevated above the level of flat triangular labrum. Mandibles straight, prognathous, longer and narrower in lectotype from Seven Weeks Poort Berg than in the Blue Berg specimens. Apex uniformly emarginate at inner margin, with sharp inward-turning points (Fig. 21B, 22A, C). Ventral process clearly marked in Blue Berg specimens, more rounded in lectotype. Surface of head distinctly punctate, punctation of mandibles hardly visible. Labrum slightly transverse, oblong; gular sulcus sharp but rather shallow.

Pronotum with some variations in details; similar but somewhat broader than in *C. izardi*. Punctation, if discernible at all, visible only at lateral and anterior margins.

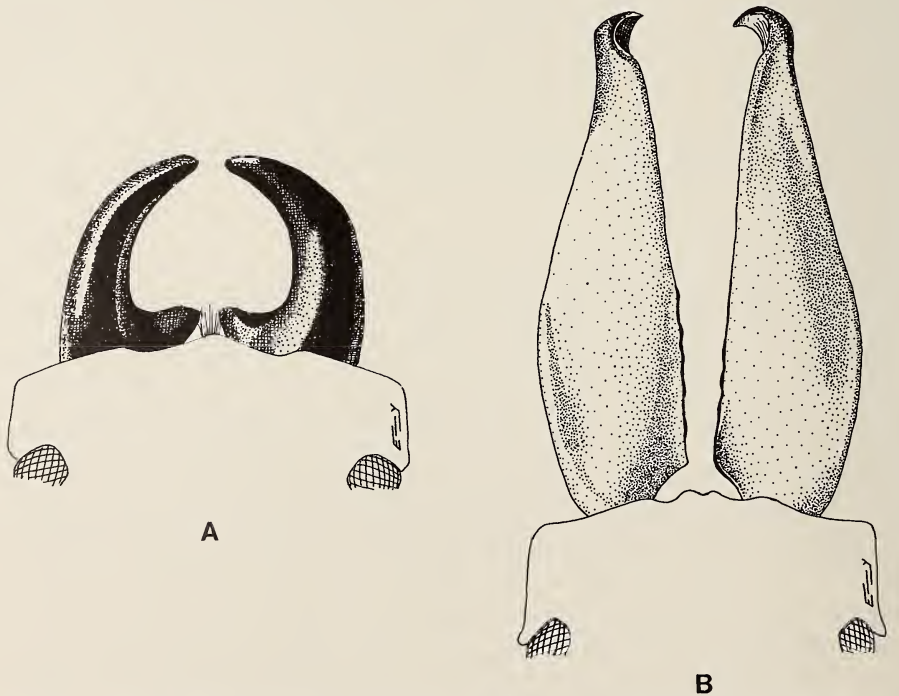


Fig. 21. Male mandibular structure in *Colophon* species. A. *C. neli* Barnard. B. *C. primosi* Barnard.



Elytra more evenly tapered towards apex, less semi-parallel anteriorly than in *C. izardi*; subhumeral carina rounded but very distinct; submarginal lateral depression coarsely corrugated transversely.

Prosternal apophysis hump-like between coxae. Anal sternite asymmetrical, off-centre apex produced in a transversely oblong and flat process.

Anterior tibia very simple, straight, with four lateral teeth and an inner apical tooth (Fig. 20A). Ventral crest serrate and continuous, without apical process. Posterior tibia consistently with a sharp lateral tooth in middle.

Aedeagus of asymmetrical type. Penis strongly sclerotized and asymmetrical. Right paramere armed at inner margin; apex (distal) truncate, acute-angled; left paramere narrower than in *C. izardi*, apical portion parallel with roundly truncate apex.

Thorax, body, elytra, and head (except vertex), black; vertex, mandibles and legs (except tarsi), reddish brown.

*Female.* Head conspicuously small (Fig. 22B). Black, but coxae, humeri, tibiae and parts of head reddish brown. More convex than in male, lateral corrugation of elytra less distinct. Prosternal process similar; anal sternite sharply punctate, punctures with fine and short hairs; anal sternite in male only finely punctured and bare.

#### *Length*

Male 28–35 mm (lectotype 35 mm); length of mandibles 8–10,5 mm (lectotype 10,5 mm); female 20–22 mm.

#### *Distribution*

Central section of Swartberg range, northern range of Cape mountains.

#### *Material examined*

5 ♂ (3 fresh, 2 damaged) (2 dissected), 7 ♀ (5 fresh, one damaged, one fragmented). Lectotype ♂, 2 ♀ paralectotypes, and additional 3 ♂ and 2 ♀ specimens in South African Museum, Cape Town; 1 ♂ and 2 ♀ paralectotypes in British Museum (Natural History), London. 1 ♀ in Transvaal Museum, Pretoria.

*Lectotype.* ♂: Seven Weeks Poort Berg, Ladysmith District, 7 000 ft. [2 134 m], K. H. Barnard, 1928; in South African Museum, Cape Town.

*Paralectotypes.* 1 ♂, 2 ♀: Seven Weeks Poort Berg, Ladysmith District, 7 000 ft. [2 134 m], K. H. Barnard, 1928; in British Museum, London. 2 ♀ (one badly fragmented): Seven Weeks Poort Berg, Ladysmith District, 7 000 ft. [2 134 m], K. H. Barnard, 1928; in South African Museum, Cape Town.

*Further material.* 1 fresh ♂, 2 damaged ♂, 2 fresh ♀: Blue Berg, Zwartberg range, 1930, F. Berrisford; in South African Museum, Cape Town. 1 ♀: Seven Weeks Poort Berg, 6 300 ft. [1 921 m], 2 Feb. 1986, coll J. Vlok; in Transvaal Museum, Pretoria.

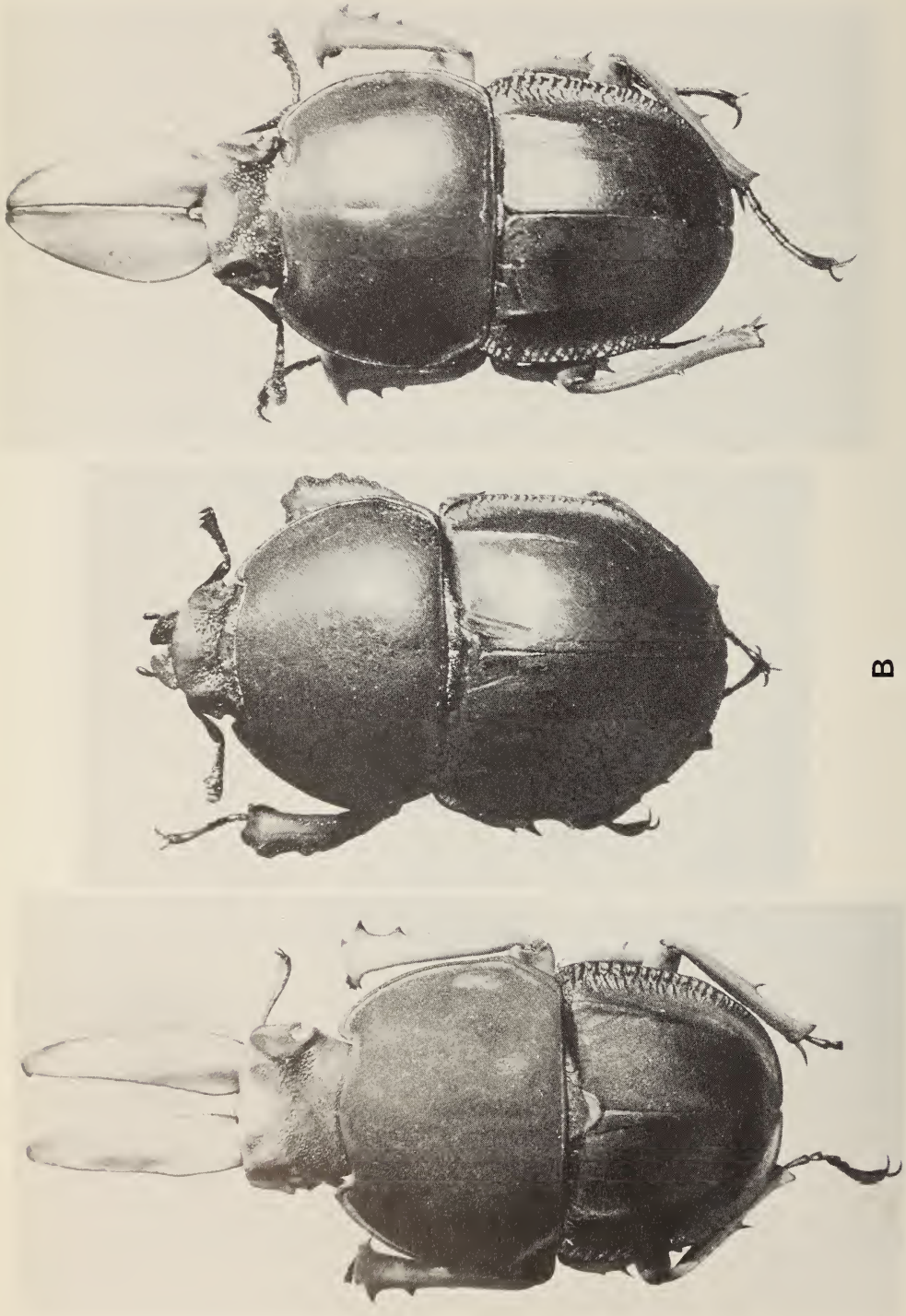


Fig. 22. *Colophon primosi* Barnard. A. Big male; paralectotype; length 35 mm. B. Female; length 22 mm. C. Small male; length 28 mm. The slight allometric variation shown here is the greatest observed in the genus.

### Remarks

*Colophon primosi* is the most peculiar species of the genus, with mandibles not readily derived from any other forms. Other characters, however, secure its place in the genus and also in the apomorphic lineage (asymmetrical aedeagus, raised clypeus).

All specimens of the type series were found dead, some of them very distinctly bleached, leaving Barnard (1929: 176) in doubt in respect of their natural coloration. Three fresh specimens (1 ♂, 2 ♀) of the Blue Berg series were probably found live and confirm the unusual coloration described by him. Male mandibles, anterior part of head, gula and all femora and tibiae light yellow-brown; rest of body, antennae and tarsi black. In females the coloration is similar, except mandibles are black in small specimens.

There is no noteworthy difference between specimens of the Seven Weeks Poort Mountain and Blue Berg samples, which raises some interesting historic biogeographic problems (see p. 362).

### *Colophon westwoodi* Gray, 1832

Figs 8, 20B, 23, 24A

*Colophon westwoodi* Gray, 1832: 533, pl. 46 (fig. 5). Castelnau, 1840: 173. Westwood, 1855: 194. Parry, 1864: 70. Péringuey, 1901: 3. Van Roon, 1910: 8. Boileau, 1913: 218. Handlirsch, 1924: 695. Barnard, 1929: 166, fig. 1; 1932a: 19, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 309, 320.

### Diagnosis

Black, medium to large size. Most of anterior margin of pronotum marginate. Mandibles short and strongly curved inward, main arm broadly bifid with rounded protuberance dorsally; ventral and dorsal process in basal position, small and roundly pointed. Anal sternite asymmetrical, aedeagus of asymmetrical type. Anterior tibia finely arcuate, dilated towards apex, with four or five lateral teeth not quite regularly increasing in size distally.

### Description

*Male*. Head broadly oblong, genal margin in front of eyes semi-parallel, occasionally finely emarginate, anterior angle sharp. Anterior margin moderately sinuate between mandibles, a canthus above clypeus sometimes more or less protuberant in middle. Vertex deflected to pre-clypeal canthus, overhanging the clypeus; latter is flush with the base of flat, triangular labrum. A somewhat similar canthus is present only in *C. primosi*. Ocular canthi flat. Vertex with a pair of anterior protuberances and an even more distinct median protuberance. Punctuation strong, dense and rather uniform. Mandible short and stout, main arm broad and short, evenly curved in about 90° towards equally broad and bifid apex. There is a large and rounded protuberance of different elevations in the middle of the dorsal surface, close to inner margin. As a small dorsal process is present near the base, it is thought that the dorsal protuberance is not analogous with the





Fig. 23. *Colophon westwoodi* Gray, male; length 20 mm.

dorsal processes of other species (Fig. 24A). Mentum almost flat, about twice as broad as long, slightly converging anteriorly, apex rounded. Transverse gular sulcus flat.

Pronotum even in large males only moderately broader than elytra, rather convex. Broadest in front of basal third, lateral margins evenly arcuate and converging anteriorly, emarginate posteriorly to sharp and rectangular posterior angle. All edges margined, margination only interrupted in middle of anterior margin. Punctuation very fine, but sharp, uniformly dense; hardly more distinct laterally.

Elytra about as long as combined breadth, semi-parallel in anterior half of length; do not appear as disproportionately small in relation to the pronotum, as in most other species. Surface smooth and matt-shagreened with eight irregular rows of fine punctures. Lateral submarginal depression more densely, but not more coarsely, punctate.

Anal sternite very distinctly asymmetrical.

Anterior tibia moderately arcuate at inner margin, evenly dilated from base to apex. Lateral margin with four or five progressively larger triangular processes; last two (largest) processes do not appear as a bifid unit (Fig. 20B). Ventral crest continuous from base to apex, not forming an apico-ventral process. Lateral median process of posterior tibia as large and sharp as in intermediate tibia (in other species usually reduced or missing).

Aedeagus of asymmetrical type. Penis strongly sclerotized, apical portion asymmetrically dilated. Right paramere produced to a large inner process; its anterior margin to apex is straight, posterior margin evenly and deeply emarginate towards base. Left paramere narrow with rounded apex.

*Female.* Distinguished by anteriorly marginate pronotum with sharply pointed rectangular posterior angle.

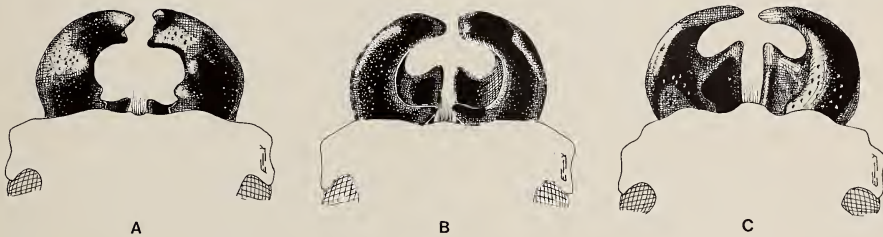


Fig. 24. Male mandibular structure in *Colophon* species. A. *C. westwoodi* Gray. B. *C. thunbergi* Westwood. C. *C. barnardi* sp. nov.

#### *Length*

Male 21–25 mm, female 19–24 mm.

#### *Distribution*

Table Mountain, Cape Town.

#### *Material examined*

14 ♂ and 19 ♀. Holotype and three additional specimens in British Museum (Natural History), London; 24 specimens in South African Museum, Cape Town, and 5 specimens in Transvaal Museum, Pretoria.

*Holotype.* ♂: no data, ex Vigin's collection, British Museum, London.

*Additional material.* The other material listed above has been recorded from Devil's Peak, Constantiaberg, Kalk Bay Mountain, and Echo Valley. Live specimens were collected in December, January and February.

#### *Remarks*

This was the first species of the genus to be described, and ever since it has been the most frequently collected.

*Colophon barnardi* sp. nov.

Figs 20E, 24C, 25

*Diagnosis*

Small black species. Mandibles with ventral process only. Anterior tibia with three apico-lateral teeth. Clypeus raised above labrum. Aedeagus of asymmetrical type.

*Description*

*Male.* Medium size, completely black. Head broadly oblong with sharp genal canthus and with rounded and arcuate elevations at the inner margins of eyes. Clypeus slightly produced and sharply elevated over labrum. Surface densely and sharply punctate, integument matt. Mandibles short, sickle-shaped, arcuate through 90 degrees. Dorsal process entirely absent, ventral processes large, their inner margins parallel; apex of processes forward-pointing, acute-angled. Apex of main arms simple (Fig. 24C). Mentum flat, hardly convex transversely, apical margin broadly arcuate. Pregular sulcus deep.

Pronotum evenly convex transversely, more deflected towards posterior than towards anterior margin. All around marginate; submarginal lateral depression very narrow anteriorly, slightly dilated at lateral angle of pronotum. Pronotum broadest at posterior third of length, gradually more arcuately contracted towards anterior lateral angle; pronotum considerably contracted posteriorly, but lateral margin straight to obtuse-angled posterior lateral angle. Disc smooth and matt with scattered punctures at lateral and anterior margins. Base of prosternal apophysis sharply dentate.

Elytra distinctly longer than combined breadth, not particularly small compared to pronotum, narrower than the latter. Humeral angle rectangular, narrowly rounded. Disc convex, submarginal depression broad anteriorly; gradually narrower behind; suture not elevated, marginate or smoother than disc. Surface entirely smooth, without any costal elements, matt with indistinct traces of scattered punctation.

Anterior tibia straight, narrowest at basal quarter of length; dilated in apical half, forming three lateral teeth; inner apical angle sharply produced (Fig. 20E). Ventral crest moderately elevated in basal half, gradually diminishing anteriorly; apico-ventral process absent.

Anal sternite asymmetrical at apical margin, forming a narrow process to the right of median line (ventral view).

Aedeagus of asymmetrical type.

*Female.* Pronotum slightly narrower, but of similar shape to that of male; disc of elytra similarly smooth (paratype) or with short, subhumeral costal element (allotype).

*Length*

Male 20 mm, female 20,2–21,0 mm.





Fig. 25. *Colophon barnardi* sp. nov., male; holotype; length 20 mm.

*Material examined*

1 ♂, 2 ♀, and 1 ♂ thorax with right leg attached. Holotype ♂ and allotype ♀ in South African Museum, Cape Town; 2 paratypes (1 ♂ thorax, 1 ♀ lacking abdomen) in Transvaal Museum, Pretoria.

*Holotype.* ♂ (dead): Leeuw River Peak, Swellendam, April 1941, K. H. Barnard.

*Allotype.* ♀ (dead): Leeuw River Peak, Swellendam, April 1941, K. H. Barnard.

*Paratypes.* 1 ♂ thorax, 1 ♀: Leeuw River Peak, Swellendam, April 1941, K. H. Barnard.

All specimens were labelled by Barnard as *C. thunbergi*.

*Etymology*

This species is named in honour of Dr K. H. Barnard, collector of most of the known specimens of *Colophon* and first reviser of this genus.

*Colophon thunbergi* Westwood, 1855

Figs 24B, 26

*Colophon thunbergi* Westwood, 1855: 198. Parry, 1864: 70; 1870: 71; 1872: 83. Boileau, 1913: 217. Barnard, 1929: 167, fig. 2; 1932b: 170, fig. 1. Didier & Séguy, 1953: 77. Brinck, 1956: 310, 320.

*Diagnosis*

Rather large, black species. Mandible with dorsal and ventral processes. Clypeus raised above labrum. Anterior tibia slender and bent at base, dilated with bifid or trifold apico-lateral armature.

*Description*

The description below is based on the holotype and points out, where necessary, the differences shown by the fragments.

*Male.* Head broad and short, angularly oblong, anterior angle of gena only slightly obtuse-angled, narrow, anterior margin not indented or emarginate near lateral angle. Anterior margin evenly sinuate in middle. Disc rather sharply raised at inner margin of eye, moderately depressed anteriorly in middle, with a pair of round and indistinct elevations at either side of depression. Punctuation consists of rather uniform, moderately large, well-spaced punctures in the middle; integument densely shagreened. Mandibles short and stout, bent more or less at a right angle; dorsal process near base conical; in the fragments less forward-pointing (as figured). Ventral process very broad, with inner corner roundly produced anteriorly, reaching about two-thirds of mandibular length (Fig. 24B). Labrum flat and pointedly triangular, clypeus sharply elevated above its base. Mentum large and flat, oblong, anterior margin truncate. Pregular sulcus evenly concave, not sharply incised.



Fig. 26. *Colophon thunbergi* Westwood, male; length 15 mm. An estimated total length of the specimen could be 25 mm.

Pronotum broadest at about basal third; margins very slightly emarginate or straight, contracting to obtuse-angled basal corner. Margination also complete anteriorly. Pronotum in the holotype evenly rounded disciform, lateral margins evenly arcuate, converging to perfectly rectangular anterior angle. Surface densely shagreened, also very finely punctured at sides.

Elytra semi-parallel at anterior portion, very slightly contracted towards rectangular humeral angle. Surface of disc smooth, densely and finely shagreened and indistinctly punctate. A much reduced subhumeral costa is slightly elevated at basal fifth of length (some further); hardly discernible longitudinal lines are shown only by smoother integument. Dimensions in holotype 11,5 x 11,8 mm.

Anal sternite distinctly asymmetrical, off-centre process flatly rounded.

Anterior tibia bent inward in dorsal view. In holotype almost the whole basal third narrow, apical dilation disciform. Apical armature bifid (Fig. 26). In all fragments the narrow basal portion is shorter, apical dilation more gradual, and the apical armature consists of three triangular processes (in one tibial fragment the proximal process is clearly broken off). Ventral crest continuous between base and apex, evenly and moderately elevated, not raised at base as in *C. barnardi*. In the latter species the tibia is more slender and much straighter.

Aedeagus of asymmetrical type.

*Female.* The single female in the British Museum, from Zuurbraak Peak, is herein tentatively retained in *C. thunbergi*. It is somewhat different from the two females from Leeuw River Peak that are herein referred to *C. barnardi* (see p. 411). The Zuurbraak Peak female differs from the Leeuw River Peak females in the following characters: ocular canthus sharper, punctation of head coarser and sparser. Elytron in the Zuurbraak specimen is marked by two punctured costae of common subhumeral origin; they reach to about the middle of the elytral length.

#### *Length*

Male (holotype) 26 mm.

#### *Material examined*

1 ♂ (holotype); 1 ♀ (identity doubtful), in British Museum (Natural History), London. 5 ♂ heads and 5 ♂ anterior legs, South African Museum, Cape Town.

*Holotype.* ♂: no locality, with labels 'Type Col. 247; *C. thunbergi* and *C. westwoodi* Gray i[n]. litt. in the Hope Museum, Oxford'.

*Additional material.* 1 ♀ (identity uncertain): Zuurbraak Peak, in British Museum, London. The 5 ♂ heads and 5 ♂ anterior legs are from Zuurbraak Peak, Langeberg Range, near Swellendam; coll. Barnard & Thorne, February 1932; South African Museum, Cape Town. These latter fragments indicate the possible locality of the holotype.

#### *Remarks*

The locality of the holotype in the Hope Museum, Oxford, is not known, but morphologically it agrees sufficiently with the fragments collected by Barnard at



Zuurbraak Peak, where *Colophon thunbergi* is sympatric with *C. izardi*. The slight differences found between the holotype and the fragments do not appear to be greater than the range observed among the fragments—with the possible exception of bifid tibial armature in holotype.

*Colophon whitei* Barnard, 1932

Figs 27D–E, 28, 29A

*Colophon whitei* Barnard, 1932b: 171, fig.3; 1932a: 20, figs; 1936: 8. Didier & Séguy, 1953: 17. Brinck, 1956: 311, 320.

*Diagnosis*

Large black species. Mandible with dorsal and ventral processes. Anterior tibia bent inward, dilated lateral margin deflected and deeply excised before reaching bifid apical armature. Anal sternite and aedeagus of asymmetrical type.

*Description*

*Male.* Head broadly oblong with sharp genal canthus. Surface longitudinally elevated at inner margins of eyes, elevations rounded and slightly inward slanting from frons towards base; a similar, broadly funnelling elevation occupies the whole frons. Frons steeply deflected to clypeus. Clypeus broad, flatly emarginate at anterior margin, showing some variation in breadth and depth of emargination; sharp anterior edge of clypeus raised above the level of labrum. Labrum flat, elongately triangular, sometimes briefly bifid at apex. Integument of head more densely and coarsely punctate in depressions than on elevations. Mandibles with dorsal and ventral processes (Fig. 29A); main arm prognathous, usually only

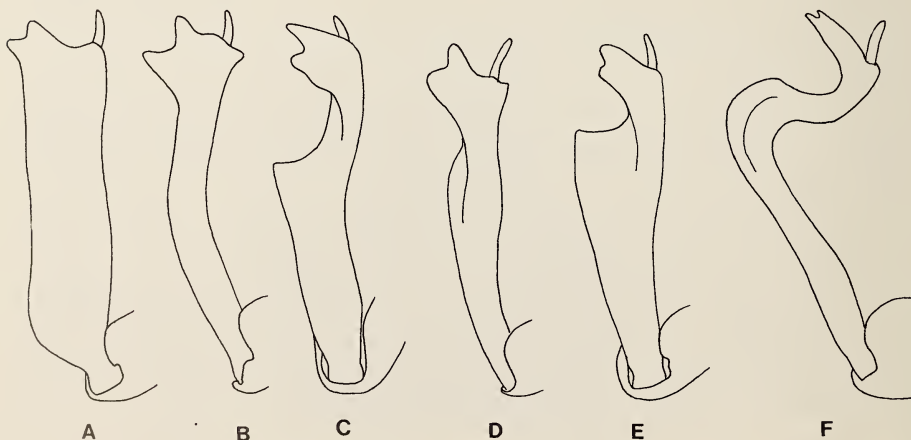


Fig. 27. Male anterior tibiae in *Colophon* species. A. *C. neli* Barnard. B. *C. montisatris* sp. nov. C. *C. montisatris* sp. nov. in lateral view. D. *C. whitei* Barnard. E. *C. whitei* Barnard, lateral view. F. *C. izardi* Barnard.

apical third curved inward through 90 degrees; apices, particularly that of the left mandible, narrow and truncate. In the inner margin of each mandible two processes appear. The ventral process seems to be homologous with that of *C. cassoni*, *C. eastmani* and *C. cameroni*, but the more dorsal one is probably not. This tooth lies in the midline of the mandible's thickness in *C. whitei*, whereas in the other three species it lies flush with the dorsal surface. This mandibular process in semi-dorsal position appears as a unique character among the known species of the genus. The most closely related species, *C. montisatris* sp. nov., entirely lacks this semi-dorsal tooth, although its ventral one is homologous with that of *C. whitei*. The rudimentary semi-dorsal process of *C. barnardi* might be homologous with that of *C. whitei*. Mentum slightly concave, lateral margins parallel, anterior lateral angles narrow; truncate anterior margin slightly produced in middle. Pregular sulcus deep.

Pronotum evenly convex transversely, more deflected to posterior than to anterior margin; broadest at the basal third of length where lateral margins are parallel; margins evenly curved towards produced anterior angle; distinctly emarginate behind; posterior angle obtuse. All margins evenly and sharply bordered, margination only interrupted in a spot in the middle of the anterior margin. Integument smooth but not shiny, with a few fine punctures laterally; disc without, or occasionally with, faint scattered punctures. Base of prosternal apophysis with a small callus. Scutellum triangular with arcuate margins showing some variation in breadth and shape.

Elytra narrower than the widest part of the pronotum but broader than the pronotum at its posterior angles. Humerus narrowly rounded, almost rectangular. Disc convex, submarginal depression broad, integument here more or less distinctly corrugated. Surface otherwise smooth, matt with fine and scattered punctation. Suture line not conspicuously raised, although sometimes smoother and shinier than rest of surface.

Anterior tibia gradually dilated from base, dilation turns gradually into a latero-ventral position; dilation is abruptly reduced at apical quarter where it forms a sharp rectangular corner; apico-lateral corner of tibia is formed by a bifid process (Fig. 27D, E). Median (primary) ventral crest distinct. Inner margin of anterior tibia almost straight. Intermediate tibia with a single, sharply pointed median process; posterior tibia unarmed.

Apical margin of anal sternite strongly asymmetrical in middle.

Aedeagus asymmetrical; right paramere with large inner process; left paramere simple, comparatively broad.

*Female.* Pronotum narrower than in males, disc similarly smooth, only punctate near lateral margins; a faint longitudinal median impression appears in some specimens. Humeral angle rounded, lateral margins finely arcuate. Surface smooth and matt with scattered, very fine punctures. No distinct costal elements. No reliable differences could be found between females of *C. whitei* and of *C. montisatris* sp. nov.



Fig. 28. *Colophon whitei* Barnard, male; lectotype; length 25,5 mm.

*Length*

Male 26–31 mm, female 19–22 mm.

*Distribution*

Central section of the Swartberg (northern range of the Cape mountains), west of Meiringspoort.

*Material examined*

15 ♂ (3 damaged, 3 bleached, 1 anterior part of body), 5 ♀, intact specimens; 5 ♂ and 2 ♀ heads.

*Lectotype.* ♂, Meiringspoort Berg, Zwartberg Range, Febr. 1932, K. H. Barnard and C. W. Thorne; South African Museum, Cape Town.



*Paralectotypes*. 8 ♂ and 5 ♀, Meiringspoort Berg, Zwartberg Range, Febr. 1932, K. H. Barnard and C. W. Thorne. (Of these 7 ♂ and 1 ♀ in South African Museum, Cape Town, and 1 ♂ and 2 ♀ in British Museum, London.) 6 ♂ and 5 ♀ heads: Meirings Poort Berg, Zwartberg Range, [6 500 ft. (= 1 982 m), March] 1931, A. B. Berrisford; 1 ♀ (data as for holotype) does not belong to this species; 1 ♂, 2 ♀: Blesberg, Zwartberg Range, 1930, F. Berrisford (locality probably erroneous; see below), in South African Museum.

#### Remarks

This and the following species (*C. montisatris* sp. nov., p. 418) are closely related and their separation might have occurred only after the present populations retreated to the high altitudes of the Swartberg Range, on either side of Meirings Poort. It is evident that the common ancestor had a distribution area on the flat at the level of the foot of the mountain, since Meirings Poort cuts through the latter and serves to drain water from the north to the south.

The locality date for the specimens recorded from Blesberg must be regarded as doubtful. These three specimens formed part of Barnard's (1932*b*) type series. However, Blesberg is on the east side of Meiringspoort. The identity of the females could not be ascertained, but the male is certainly conspecific with the rest of the type series of *C. whitei* from the west side of Meiringspoort. Blesberg is the type locality of *C. montisatris* sp. nov., where 10 ♂ specimens (2 anterior parts of body) of that species were collected in 1979 and 1981 without finding any fragments of *C. whitei*. It seems to be almost certain that at least the male specimen of *C. whitei* recorded from Blesberg is incorrectly labelled, and was actually collected on the west side of Meiringspoort. Similar problems were encountered with material of *C. stokoei* (see p. 393), where the possibility of erroneous locality labelling made the final evaluation of *C. stokoei* morphs impossible. It has to be taken into consideration that a considerable portion of *Colophon* specimens were collected by non-entomologist mountaineers.

A female specimen labelled as *C. whitei*, and with the same locality data as the lectotype, does not belong to this species.

Specimens mentioned in the Barnard's (1932*b*) description as collected at Blou Punt (Blaauw Punt) and Spitzkop (both on the west side of Meiringspoort), could not be found in the South African Museum, nor in the British Museum, although there is no record that Barnard disposed of any specimens to any other museums.

#### Variability

In evaluating the characters of 14 complete males, one pronotum and head, and seven heads, the variability in main characters, such as mandible, mentum and anterior tibia, was found to be minimal. No allometric variation was found between the biggest and smallest specimens, except the relatively greater breadth of pronotum in the larger specimens. In the type series there is a specimen with rather distinct longitudinal striation of elytra, which gives the impression of an

ontogenetic anomaly. A certain ontogenetic anomaly is shown in another specimen in which the right mandible is about half normal size, and having reduced but distinct male characters—and not partially hermaphrodite as is found occasionally in Lucanidae. Would the two malformations in 14 specimens indicate the genetic effect of in-breeding in a tiny extant population?



Fig. 29. Male mandibular structures in *Colophon* species. A. *C. whitei* Barnard. B. *C. montisatris* sp. nov. C. *C. izardi* Barnard, semi-lateral view.

*Colophon montisatris* sp. nov.

Figs 1, 4, 27B–C, 29B, 30A–B

*Remarks*

*Colophon montisatris* is a sister species of *C. whitei*. In many respects the new species seems to be the more ancestral and, in its characters, closer to the hypothetical common ancestor. Characters not described below were found to be identical with those described for *C. whitei*.

*Description*

*Male*. Declivity of frons towards clypeus not quite vertical; clypeus broader, distinctly emarginate. Labrum similar. Mandibles with ventral process only (the most diagnostic specific character). Main arms of mandibles slightly shorter than in *C. whitei*, not tapering towards broader apex. Ventral process sharply pointed, less produced, and altogether closer to base than in *C. whitei* (Fig. 29B).

Mentum, pronotum and elytra very similar to those of *C. whitei*.

Anterior tibia angularly nicked inward in middle, in dorsal view semi-parallel, not dilated towards apex. Lateral crest more deflected ventrally, narrower, anterior emargination towards bifid apico-lateral process deeper (Fig. 27B, C).

Aedeagus similar to that of *C. whitei*, but left unarmed paramere narrower.

*Female*. No characters could be found that enable one to distinguish between females of this species and those of *C. whitei*.

*Length*

Male 23–27,8 mm (breadth 11–14 mm), female 23 mm.

*Material examined*

10 ♂, 1 ♀ and 2 ♂ anterior bodies. Holotype ♂, allotype ♀ and 6 ♂ paratypes in Transvaal Museum, Pretoria; 1 ♂ paratype each is deposited in the South African Museum, Cape Town, British Museum (Natural History), London, and Natural History Museum, Budapest.

*Holotype*. ♂, Swartberg Range, Blesberg, 2.III.1979, leg. Endrödy-Younga, E-Y:1556.

*Allotype*. ♀ (dead), Swartberg Range, Blesberg, 6.III.1981, E-Y:1755.

*Paratypes*. 4 ♂, Swartberg Range, Blesberg, 2.III.1979, leg. Endrödy-Younga, E-Y:1556. 1 ♂ (dead): Swartberg Range, Blesberg, 6.III.1981,



Fig. 30. *Colophon montisaris* sp. nov. A. Holotype, male; length 25 mm. B. Allotype, female; length 23 mm.



E-Y:1755. 1 ♂ (dead) and 1 ♂ anterior body: Swartberg Range, Blesberg, 17.XII.1978, E-Y:1534. 1 ♂ live and 1 ♂ dead, Swartberg Range, Blesberg, 5.III.1981, E-Y:1754. 1 ♂ live, 1 ♂ anterior body, Swartberg Range, Blesberg, 7.III.1981, E-Y:1756, (3 further ♂ seen).

#### *Variation*

Allometric variation is evident from the specimens examined. The lengths (in mm) of the ten complete males are: 22,3; 23,9; 24,9; 25,0; 26,9; 27,0; 27,4; 27,5; 27,5; and 27,5. All specific characters can be found on both the smallest and largest specimens, though moderate accentuation of secondary male sexual characters was observed in large specimens. With increase in size mandibles become larger with sharper edges; ventral process, flush with main arm at ventral surface in small specimens, is produced ventrally in large specimens; pronotum becomes broader and proportionately bigger than elytra. There is no distinct difference in anterior tibia between small and large specimens.

#### *Colophon izardi* Barnard, 1929

Figs 2, 3, 27F, 29C, 31A–B

*Colophon izardi* Barnard, 1929: 173, fig. 8; 1932a: 20, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 310, 320.

#### *Diagnosis*

Male anterior tibia narrow and bent inward at 90 degrees. Armature of male mandibles forms a funnel in closed position. Pronotum in both sexes usually with a pair of red dots.

#### *Description*

*Male.* Head broadly oblong, gena emarginate in front of eye, anterior angle narrow, obtuse-angled. Ocular canthus distinct but rounded, disc broadly depressed in between. Punctuation denser and coarser laterally. Frons only slightly deflected towards clypeus, which is visible in dorsal view. Clypeus broad, finely emarginated and sharply raised above level of labrum; labrum flat and broadly triangular. Mandibles very characteristic: main arms simple, sickle-shaped, with flat dorsal surface. Ventral process reaches maximum development in this species; in dorsal view as much produced as main arms, broad from the base, the whole mandibular structure forming a funnel towards clypeus (not towards the mouth, which is beneath) (Fig. 29C). Gula broadly rounded, gular sulcus sharp and deep.

Pronotum as long as elytra, slightly broader than latter, bearing a pair of large, round centrally bilateral reddish-brown patches. Broadest at basal third, flatly and evenly curved anteriorly, evenly tapering behind, not emarginate prebasally. All edges margined, only briefly interrupted in middle of anterior margin. Punctuation very fine and scattered but distinct, stronger laterally.

Elytra with fine subhumeral crest, extending from base to middle of elytron.

Anal sternite asymmetrical, produced apex not calloused.

Anterior tibia apomorphic in shape: anterior third bent 90° inward; ventral crest low and continuous, lateral crest dilated pre-apically, then sharply interrupted, emargination between lateral crest and undivided apico-lateral process deeply U-shaped (Fig. 27F).

Aedeagus of asymmetrical type. Penis strongly sclerotized, asymmetrical. Right paramere armed inwards; inner process similar, but apex rectangular and not acute-angled as in *C. whitei*. Left paramere angularly emarginate at inner margin.

*Female*. Punctuation of head, pronotum and elytra much more distinct than in male. Inner margin of anterior tibia evenly curved. Anal sternite symmetrical, densely punctate and finely pubescent, whereas in male it is smooth and bare. Discoidal red patches of pronotum similar to male.

*Length*

Male 21,8–25,3 mm, female 20–21 mm.

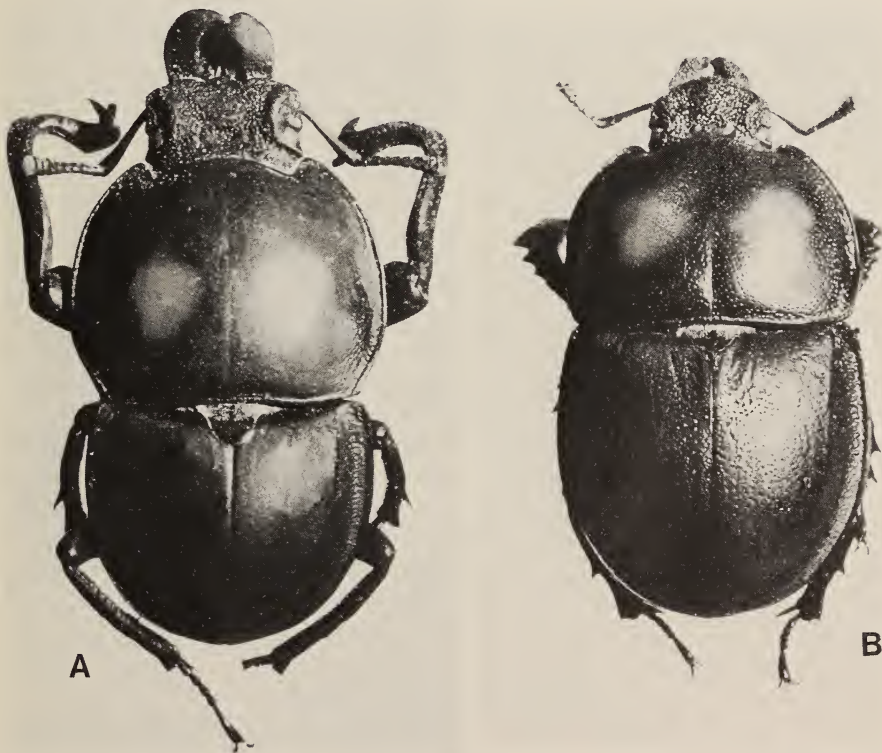


Fig. 31. *Colophon izardi* Barnard. A. Male; length 22,5 mm. B. Female; length 19,5 mm. The first live specimen found during this project.

*Distribution*

Central section of Langeberg Range, the southern range of the Cape mountains.

*Material examined*

5 ♂, 5 ♀; 17 ♂ heads, 1 ♀ head; 17 ♂ anterior tibia, 2 ♀ anterior tibia. Complete specimens are in the British Museum (Natural History), London; South African Museum, Cape Town; and Transvaal Museum, Pretoria.

*Lectotype*. ♂: Lemoenshoek, Heidelberg, C.P., 5 000 ft. [= 1 524 m], K. H. Barnard; British Museum (Natural History), London.

*Paralectotypes*. 3 ♀: Lemoenshoek, Heidelberg, C.P., 5 000 ft. [= 1 524 m], K. H. Barnard (1 ♀ in British Museum, London; 2 ♀ in South African Museum, Cape Town).

*Additional material*. 1 ♂: Lemoenshoek, January 1957, T. P. Stokoe. 2 ♂ pronota: Grootberg, Langeberg, 1.XI.1978, Endrödy-Younga, E-Y:1499. 1 ♀: Grootberg, Langeberg, 7.12.1978, E-Y:1527. 3 ♂, 1 ♀: Grootberg, Langeberg, 8.III.1979, E-Y:1562.

*Remarks*

Some females, due to their entirely black pronota, were excluded from the type series by Barnard, as were some fragments from localities from where no complete males were known. These included 3 ♀, 8 ♂ heads and 7 ♂ anterior legs, Riversdale Mountains, tops of peaks (Kampsche Berg in Barnard's description); 1 ♀, Zuurbrak Peak, Swellendam Dist., 5 000 ft. [= 1 524 m], K. H. Barnard, Oct. 1925; 9 ♂ heads, 1 ♀ head, 10 ♂ and 2 ♀ anterior legs: Tradouw Peak, Swellendam Distr., 4 400 ft. [= 1 341 m], K. H. Barnard, Oct. 1928.

It is remarkable that specimens with red pronotal dots came only from the Lemoenshoek-Grootberg area (11 specimens), and specimens with the pronotum entirely black from Kampsche Berg and Zuurbrak Peak. A final decision on the status of the black specimens is further complicated by the fact that they are all females, which are in any case difficult to identify. However, male mandibles and anterior legs from these localities do not show any difference when compared to the type specimens. Furthermore, one of the male specimens collected live in Grootberg (E-Y:1562) shows a very definite reduction of the red marking of its pronotum. The dots in this specimen are hardly more than 1 mm in diameter and dark reddish brown. Though further material would be of great interest, I have little doubt that the black-pronotum specimens are *C. izardi* Barnard.

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